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Environment Canada   Environnement Canada

Occasional Paper
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Abstract

This report is a compilation of eight research projects conducted cooperatively by the Government of the Northwest Territories Wildlife Service, the Canadian Wildlife Service, and Agriculture Canada on the ecology of bison and the forage potential of the Slave River lowlands (SRL) for livestock production. The SRL include more than 800 000 ha of alluvial flatlands located between Great Slave Lake and the 60th parallel and support a population of plains bison – wood bison hybrids that originated by emigration from Wood Buffalo National Park (WBNP) in the 1940s.

The SRL bison population experienced a major decline from 1974 to 1982 caused by a combination of mortality factors, of which predation by wolves, human hunting, and disease were the most important. Of the approximately 191 adult and subadult bison lost from March 1976 to the end of March 1977, wolf kills accounted for about 60 (31%) and hunter kills, 75 (39%). Resident and non-resident hunting seasons were closed in 1977 and a wolf control program removed 72 wolves during the winters of 1977-1979. In spite of this, the reduced bison population continued to decline. Disease causes an unknown amount of mortality. The tuberculosis infection rate in bison varied from 25 to 40% in the SRL and averaged 40% in WBNP. Brucellosis infection rates averaged 38 and 30% in the SRL and WBNP, respectively. Eradication of tuberculosis and brucellosis would likely require the elimination of all bison in the SRL and WBNP. Anthrax has caused direct losses of at least 1098 bison in the SRL and WBNP since it first appeared in 1962. It probably cannot be eradicated from the area.

Calf production in the SRL bison was the poorest reported for bison in North America. In 1978, less than 50% of mature cows produced calves and only 70% of those calves survived to the end of June. Recruitment of yearlings averaged less than 4% of the population per year from 1973 to 1979.

Quantity of native vegetation in the SRL varied greatly each year but was not limiting to bison production. Generally, wet meadows produced greater amounts of higher quality vegetation than dry meadows, and bison preferred wet meadows for grazing. Cereal crops could only be grown for green feed or silage because summer frosts prevented maturation of cereal grains. The best strategy for production of native hay would be to harvest wet meadows during mid- to late July, which would represent a compromise between quality, yield, and the technical difficulty of cutting hay on wet sites.

Bison appear to be better adapted to the SRL environment than cattle because of superior digestion of native forages, a greater cold tolerance, and better foraging ability in winter. The potential for cattle production in the SRL is questionable because of the many hazards and constraints such as incidence of diseases in wild bison, presence of predators, prevalence of insect pests, poor quality native vegetation, the long winter feeding period, and the implications of excessive soil salinity for domestic crop production. In addition, cattle ranching would also be limited by economic and sociological factors.

The results of our studies do not support extensive agricultural development of the SRL. Strategies for increasing animal production in the SRL, other than conventional cattle ranching, include management of bison as a wildlife resource and single or mixed-species grazing systems for commercial production of wild species. A pilot study ranch may be required to fully assess the feasibility of developing a mixed-species grazing system for commercial production of wild animals. Management to increase numbers of wild bison in the SRL would likely require the control of diseases, the regulation of hunting, and possibly the control of predators.

Résumé

Le présent rapport constitue une compilation de huit travaux de recherche réalisés conjointement par le Service de la faune du gouvernement des Territoires du Nord-Ouest, le Service canadien de la faune et Agriculture Canada sur l'écologie du bison et les possibilités de production de fourrage dans les basses terres de la vallée de la rivière des Esclaves en vue de l'élevage de bovins. Ces basses terres de plaines alluviales, situées entre le Grand Lac des Esclaves et le 60e parallèle, couvrent plus de 800 000 ha. Depuis les années 1940, elles hébergent une population d'hybrides du Bison des Plaines et du Bison des bois, qui ont émigré du parc national de Wood Buffalo.

Cette population a beaucoup décliné de 1974 à 1982 en raison de divers facteurs de mortalité, dont les trois principaux sont le loup, l'homme et la maladie. De mars 1976 à la fin de mars 1977, la population a perdu près de 191 adultes et jeunes adultes: environ 60 (31 %) du fait du loup et 75 (39 %) tués par les chasseurs. Les saisons de chasse pour les résidents et pour les non-résidents ont été supprimées en 1977, et un programme de contrôle de la population de loups a permis d'abattre 72 loups au cours des hivers 1977 à 1979. Malgré ces mesures, la population de bisons a poursuivi son déclin. La maladie provoque la mort d'un nombre indéterminé d'animaux. Ainsi la tuberculose atteignait entre 25 et 40 % de la population des basses terres et près de 40 %, en moyenne, de celle du parc national de Wood Buffalo. Le taux de brucellose y était respectivement de 38 % et de 30 %. Seule la disparition complète de tous les bisons de ces deux régions pourrait sans doute assurer l'éradication de ces deux dernières maladies. La fièvre charbonneuse a aussi tué au moins 1 098 bisons des basses terres et du parc, depuis son apparition en 1962. Il est probablement impossible de supprimer de ces régions toute trace de la maladie.

Le taux de natalité du bison dans les basses terres est le plus faible en Amérique du Nord. En 1978, moins de 50 % des femelles matures ont mis bas et seulement 70 % des nouveau-nés ont survécu jusqu'à la fin juin. De 1973 à 1979, les bisons âgés d'un an comptaient, en moyenne, chaque année, pour moins de 4 % de la population.

La quantité de végétation naturelle a énormément varié d'une année à l'autre dans les basses terres, sans constituer toutefois un facteur limitant du bison. De façon générale, les prés humides ont produit davantage de végétation naturelle, et d'une meilleure qualité, que les prés secs et constituaient le pâturage de prédilection des bisons. Les céréales ne se prêtaient qu'à l'utilisation en vert ou à l'ensilage, les gels de l'été empêchant la maturation des grains. Pour produire le foin indigène, le mieux serait de le récolter sur les prés humides pendant la seconde moitié de juillet, ce qui représenterait un compromis entre la qualité, la production et la difficulté que pose la fauche sur terrain humide.

Le bison semble mieux adapté que les bovins aux basses terres de la vallée en raison de sa plus grande capacité de digérer les fourrages naturels, de sa plus grande résistance au froid et de sa plus grande aptitude à se trouver du fourrage en hiver. Il est douteux que l'on puisse élever des bovins dans la région, étant donné les nombreux dangers et contraintes comme les maladies dont sont atteints les bisons sauvages, la présence de prédateurs et d'insectes nuisibles, la médiocrité de la végétation naturelle, le long hiver, les conséquences de la salinité excessive du sol pour la culture. Les possibilités d'élevage de bovins seraient en outre limitées par des facteurs d'ordre économique et sociologique.

Les résultats des études présentées dans le rapport ne justifient pas l'adoption d'une politique d'agriculture extensive des basses terres. Mis à part l'élevage de bovins selon la méthode traditionnelle, on pourrait accroître la production animale des basses terres par l'aménagement de la ressource faunique que constitue le bison et en mettant en place des systèmes de pâturage en vue de la production commerciale d'une ou de plusieurs espèces sauvages. Il y aurait peut-être lieu de créer une ferme d'élevage expérimentale afin de pleinement évaluer la faisabilité de l'établissement de ce dernier type de système de pâturage. L'accroissement du nombre de bisons sauvages dans les basses terres nécessitera vraisemblablement l'adoption de mesures de lutte contre les maladies, de limitation de la chasse et, possiblement, de contrôle de la prédation.

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Introduction

Hal W. Reynolds
Alexander W.L. Hawley

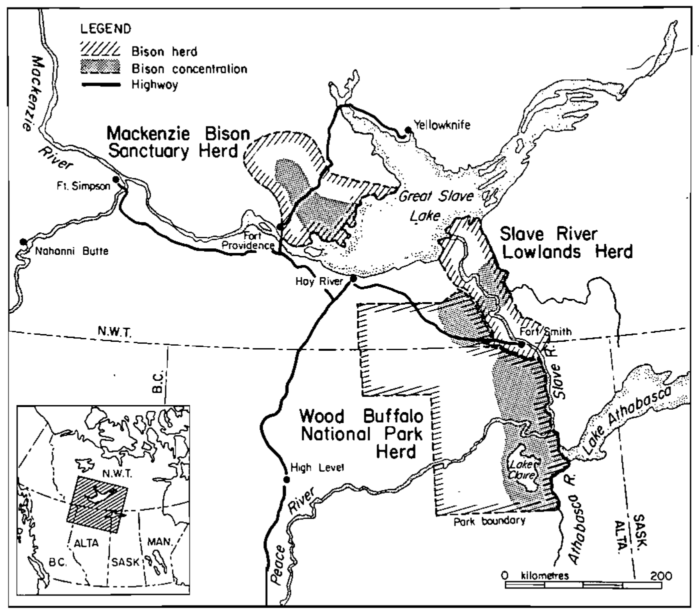
1. Background

In the 1970s, public interest in the Slave River lowlands (SRL) was focused on its potential for livestock production and revitalization of a declining resident hybrid bison population (cross between wood bison, *Bison bison athabascae,* and plains bison, *B. b. bison*). The potential conflict between these two animal production strategies, and a desire to establish management guidelines for all bison ranges in the Northwest Territories, led the Government of the Northwest Territories (GNWT) to request in 1973 that the Canadian Wildlife Service (CWS) participate in a research project. The CWS, in turn, asked Agriculture Canada, which had already been assessing the potential of the SRL for the commercial production of beef cattle, to cooperate in the study. The three agencies split up the task of assessing the value of northern meadows to native bison and domestic livestock and of providing guidelines for land management. This compilation presents data on the ecology of bison and the forage potential of the SRL for livestock production in a series of research papers prepared by participants in the cooperative project. Consideration was also given to the biological potential of the area for production of native wild bison as opposed to the production of domestic livestock. However, before a comprehensive land-use evaluation of the SRL can be completed, additional information is required on the potential to increase production of bison as a wildlife resource under existing conditions, the potential to commercially ranch bison under intensive management, the economics of various production strategies including game ranching, and the socioeconomic impact of all alternatives. This report provides valuable background information for a land-use evaluation of the SRL.

2. Status of bison in northern Canada

Populations of wild, free-ranging bison are found in three areas in northern Canada: the SRL, Wood Buffalo National Park (WBNP), and the Mackenzie Bison Sanctuary (MBS) (Fig. 1). WBNP was established in 1922 as a preserve for protection of the northern wood bison that numbered between an estimated 1500 and 2000 animals at that time (Seibert 1925, Raup 1933, Lothian 1976). However, during 1925–28, 6673 plains bison were introduced to WBNP from Wainwright, Alberta, and subsequently mixed with the resident wood bison. All bison in WBNP are now considered to be hybrids. The SRL population is believed to have originated from bison emigrating out of WBNP during the 1940s (Fuller 1950). Those bison are believed to be hybrids also. The MBS population was established in 1963 by transfer of

Figure 1
Location of three major free-ranging populations of wild bison in northern Canada

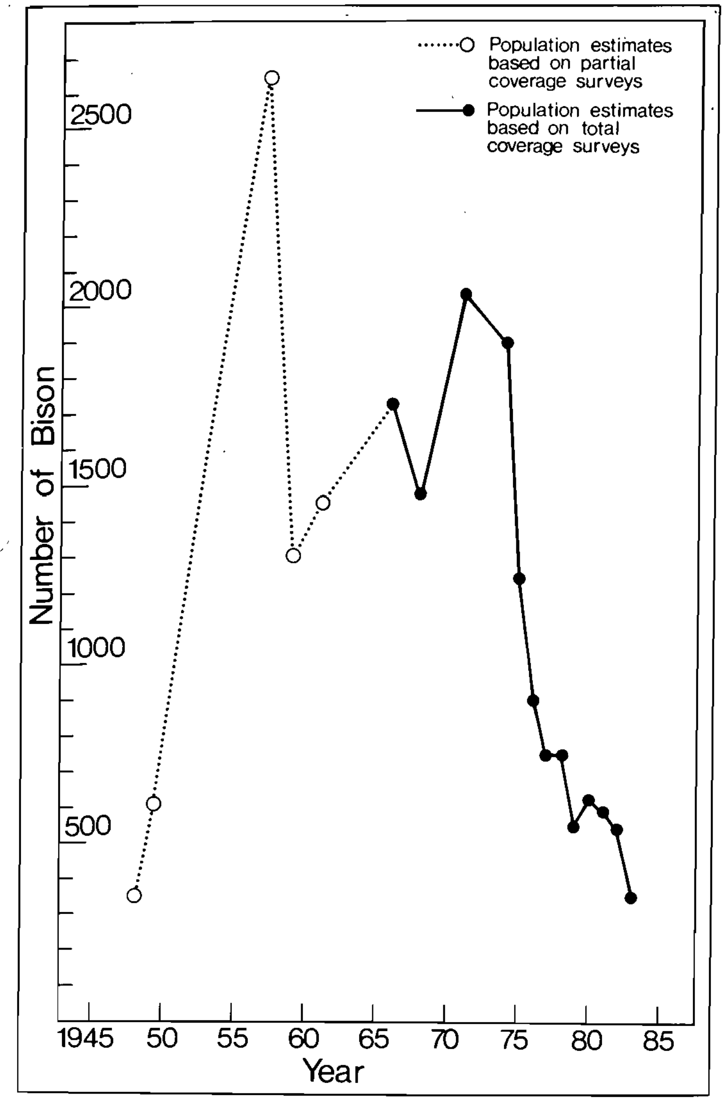


18 wood bison from the Nyarling River herd in WBNP to an area northeast of Fort Providence, NWT (Novakowski 1963).

In the SRL, bison numbers generally increased between 1948 and 1971 but declined dramatically after 1974 (Fig. 2). Van Camp (1978*a*) believed that a combination of human hunting, wolf (*Canis lupus*) predation, and disease contributed to that decline. The decline continued in spite of the removal of 72 wolves during 1977–79 (Jalkotzy 1979) and the closure of recreational hunting in 1977. At least 1202 bison were reported killed by hunters in the SRL in the 9 years 1968–76, an average of 134 bison per year. During 1973–76, at least 8–10% of the population was killed by hunters each year. That level dropped to approximately 5–6% of the population when recreational hunting was stopped in 1977. However, levels of kill by residents of the NWT who hold a General Hunting Licence (GHL)[1], continued to exceed the mean estimated 3.9% annual recruitment rate recorded between 1973 and 1979 (Van

[1] In most cases, a General Hunting Licence is issued to a member of a family or group which hunted lawfully in the NWT prior to 30 June 1953. This person may be status or non-status Indian, Métis, Inuit (Eskimo), or non-native. The General Hunting Licence allows preferential access to game animals.

Figure 2
Numbers of bison in the SRL from 1948 to 1983



Camp and Calef, this publication). Since 1977, hunting pressure alone has been sufficient to cause the population to decline. The Hook Lake segment of the SRL population, located on the east side of the Slave River, decreased to a low of approximately 310 animals by February 1982 (Hawley *et al.* 1982).

In 1891, Ogilvie (1893) estimated the total population of wood bison near an all-time low of about 300. When WBNP was established in 1922, the population had increased to approximately 1500 (Seibert 1925). After the introduction of more than 6000 plains bison by 1928, the total number of bison in WBNP continued to increase to about 12 000 animals by 1934 (Soper 1941). Later estimates put the population at between 10 000 and 12 500 animals in 1949 (Fuller 1950), between 8000 and 12 000 during the 1950s and 1960s (Novakowski 1961), and about 9200 in 1972 when systematic aerial surveys were initiated (Carbyn *et al.* 1987). (Population estimates done before 1972 were based on partial surveys and may not have been accurate.) An unusual flood in the Peace–Athabasca Delta during spring 1974 drowned an estimated 3000 bison, causing a major decline in the park population. By 1975, the population had been reduced to 5500. Recently, the number of bison in WBNP has fluctuated between 4000 and 5000 and has remained relatively stable within those limits (Carbyn *et al.* 1987). Present studies focus on why the population is not increasing. Hunting of bison in the park is illegal and has never been a significant mortality factor, despite some poaching. Carbyn *et al.* (1987) consider wolf predation to be the major cause of bison mortality in the park; however, the high incidence of diseases, such as brucellosis and tuberculosis (Broughton, this publication), may be limiting animal production.

Pure wood bison were considered extinct by 1950; however, in 1957 an isolated population of bison was observed in the Nyarling River and Buffalo Lake areas in the northwest corner of WBNP. After detailed examination of collected specimens, Banfield and Novakowski (1960) classified that herd as morphologically characteristic of wood bison and CWS decided to save the wood bison from possible extinction. That decision led to the present-day CWS program for the rehabilitation of wood bison (Reynolds *et al.* 1982).

In the MBS, the introduced herd of wood bison has increased exponentially from the initial 18 animals transferred there in 1963 from the Nyarling River population (Fuller and Hubert 1981, Calef 1984). By 1984, the MBS population exceeded 1200 animals and it now exceeds 1500 (C. Gates, pers. commun.). The growth rate of this herd has been near the maximum rate of increase for bison under natural conditions in northern environments (Calef 1984). Several factors, including protection from hunting, low incidence of disease, and lack of predation by wolves, are believed to be the major reasons for the rapid population growth. The wood bison in the MBS have been expanding their range in a northwesterly direction beyond the present boundary of the sanctuary. The NWT government (1983) drafted a 10-year management plan for that herd, including a proposal for hunting, and invited comments from the public. The management plan was published in June 1987.

3. Agricultural interest

There has been considerable public interest in developing the SRL for agriculture for many years. In 1955, a reconnaissance of soils and topography in the area showed that an estimated 73% of the lowlands were potentially suitable for agriculture. However, the survey team concluded that economic limitations precluded extensive agricultural development at that time (Day and Leahey 1957). Continued interest in agricultural development and numerous applications for grazing leases stimulated what was then the Department of Northern Affairs and National Resources at Fort Smith to request the federal Department of Agriculture to further evaluate the agricultural potential of the SRL. During summer 1965, several researchers conducted economic appraisals and examined the vegetation and soils of the lowlands (Stutt 1968, Stutt *et al.* 1969, Day 1972). Stutt (1968) speculated that beef cattle ranching, based on a minimum unit of 15 km^2 of range, had potential for economic success. However, Stutt (1968) also recommended that agricultural development should not proceed prior to receiving data from experimental trials because of the potential for numerous physical and economic limitations. The subsequent policy presented by Stutt *et al.* (1969) was as follows:

> The Government of Canada is committed to a policy of removing from agriculture those areas that are submarginal and cannot provide a reasonable economic return to the farmer, even under relatively favorable market conditions. On the basis of an evaluation of all pertinent factors, the committee cannot

find a basis for encouraging, or even permitting, development of the area [SRL] by private enterprises at the present time.

However, those researchers stated that limitations imposed by isolation, competing markets, and economics would be subject to change with time, leaving the door open for future evaluation.

Increasing public pressure to develop the SRL for agriculture led Agriculture Canada to decide in 1968 to assess climatic limitations to the production of domestic crops and the productivity and quality of native vegetation for commercial cattle ranching. Their 7-year (1968–74) research project at Grand Detour on the Slave River was designed to estimate the potential of the SRL to produce pasture, hay, and grain and to support commercial production of beef cattle. Prior to completion of this study, Day (1972) reported that the majority of soils in the SRL appeared suitable for agriculture, thereby necessitating an investigation into what other limitations, if any, there were to a viable agricultural industry. Pringle (this publication) reports the results of the Grand Detour study.

4. Present land use

Use of land is controlled by regulations under the Territorial Lands Act, federal legislation administered by Indian and Northern Affairs Canada. Use of wildlife is controlled by regulations under the Wildlife Act, a territorial statute administered by the Department of Renewable Resources, GNWT. Trapping is currently identified as the main land use in the SRL, although small-scale timber and fuel wood harvesting also occurs. A GHL holder has the right to hunt or trap game for food or pelts on unoccupied Crown lands in the NWT as long as the species hunted has not been declared under the NWT Act to be in danger of extinction. In addition, GHL holders have access to some endangered species under the terms of quotas. The bison of the SRL are not listed as an endangered species in the NWT Act because they are classified as hybrids, whereas wood bison in the MBS are on the list and are protected. In 1975 Indian and Northern Affairs Canada and the GNWT imposed a moratorium on the leasing of land for agricultural development in the NWT that is still in effect, awaiting settlement of aboriginal land claims and the formulation of agricultural and land-use policies.

5. Cooperative research project

Applications for agricultural leases and the hunting of bison by resident and non-resident hunters increased during the early 1970s, making the survival of the SRL bison population uncertain. In addition, the question of agricultural development in the SRL had not been resolved. Therefore, in 1973 the GNWT developed a cooperative research project involving its Game Management Division, the CWS, and Agriculture Canada. Its main objectives were to assess the value of sedge-grass meadows of the SRL to resident bison populations and introduced domestic livestock, and to provide guidelines to federal and territorial governments for land management within bison ranges on the SRL (Simmons 1974). The project also identified the need to develop a management plan for bison in the NWT, as well as the need to develop an agricultural policy. The specific responsibilities of each agency were as follows (all references are to this publication):

1. Population dynamics of bison (GNWT; Van Camp and Calef).
2. Seasonal movements and distribution of bison by herd, sex, and age class (GNWT; Calef and Van Camp).
3. Factors limiting bison productivity (GNWT and CWS; Calef and Van Camp, Van Camp and Calef, Van Camp, Broughton, Reynolds and Peden):
   a) Predation (GNWT; Van Camp),
   b) Diseases and parasites (CWS; Broughton),
   c) Hunting (GNWT; Van Camp and Calef, Van Camp),
   d) Other disturbance by humans (GNWT; Calef and Van Camp, Van Camp and Calef),
   e) Weather: snow, flooding (CWS; GNWT; Calef and Van Camp, Van Camp and Calef, Reynolds and Peden).
4. Availability, quality, and quantity of bison forage on the study areas (CWS; Agric. Can.; Reynolds and Peden; Reynolds and Hawley, *Seasonal variation in forage quality;* Pringle).
5. Food requirements of bison by season (CWS; Reynolds and Peden, Hawley):
   a) Species selected (Reynolds and Peden, Hawley),
   b) Amount of forage required (Hawley),
   c) Nutrient requirements (Hawley).
6. Efficiency of use of forage by bison (CWS; Hawley).
7. Habitat requirements of bison other than forage (CWS; not done).
8. Model of crop production on present bison habitat (Agric. Can.; Pringle):
   a) Suitability of soils,
   b) Suitability of climate,
   c) Need for and effects of cultivation,
   d) Need for and effects of flood control,
   e) Market for agricultural products.
9. Model for livestock production on present bison ranges (Agric. Can.; Pringle):
   a) Value of native forage,
      i) Ability to use native forage,
      ii) Need for supplemental nutrients,
   b) Need for wildlife control or eradication,
   c) Other limiting factors (flooding, insects) and cost of controls,
   d) Markets for livestock.
10. Finding of substitute bison ranges away from areas proposed for farming (CWS; not done).
11. Economics of bison production (GNWT; not done).

This Occasional Paper compiles the data collected in the cooperative research project, and, for comparison, includes information drawn from other studies.

Description of the Slave River lowlands

Hal W. Reynolds

1. Location

The Slave River lowlands (SRL) are situated in the southwestern part of the Northwest Territories (NWT) and comprise approximately 832 000 ha (Day 1972) located between the Taltson and Tethul Rivers on the east and the Little Buffalo River on the west, and between Great Slave Lake on the north and the 60th parallel on the south (Fig. 1). The north-flowing Slave River roughly bisects the region. The major part of the bison and wolf research study area (Hook Lake) is located on the east side of the Slave River in an area lying between the Rat River on the north and Brulé Point (on the Slave River) on the south. Research activities were conducted out of the Hook Lake base camp. The main portion of the agricultural research study area (Grand Detour) is located on the west side of the Slave River (Fig. 1).

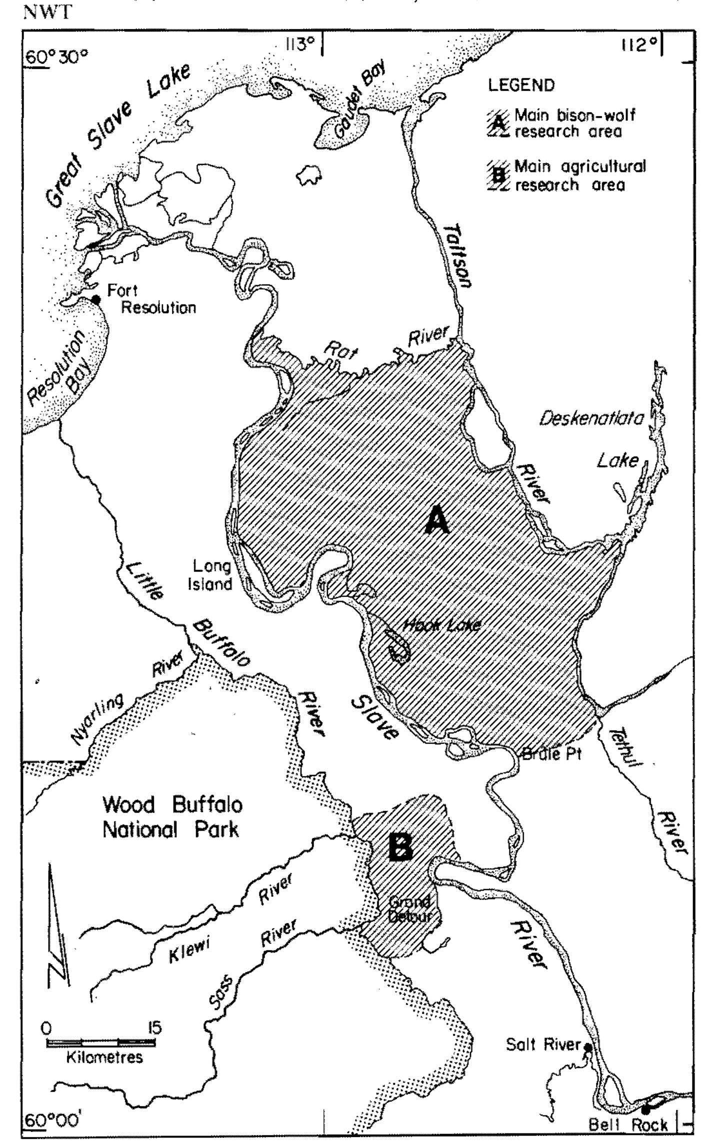
2. Topography and physiography

The SRL consist of alluvial flats bordered by low benchlands and terraces that develop into rolling uplands with isolated ridges and low hills (Rowe 1972). The area lies in the Great Slave plain portion of the Interior Plains Province, one of the physiographic divisions of the southwestern part of the NWT (Day 1972), and is characterized by low-lying, flat land with numerous lakes and abandoned stream beds. The elevation of the lowlands decreases from about 207 m at Fort Smith in the south to about 158 m at Fort Resolution in the north. Most of the lowlands are underlain by Middle Devonian rocks containing gypsum, salt, limestone, and breccia in their basal strata, and dolomite and limestone in their upper strata (Day 1972). Most of the bedrock is deeply buried under glacial tills and under alluvium from periodic flooding of the Slave River (Rowe 1972). The lowlands are maintained in a dynamic state because of frequent blocking of the Slave River by ice, with consequent flooding and erosion of the river banks.

3. Climate

The climate of the Mackenzie River plain, which includes all of the SRL, is continental, subject to irregular extremes of weather, and similar to that in the agricultural belt in the lower Peace River region in north-central Alberta (Harris and Carder 1975). Precipitation is highly variable and limits crop production (Harris and Carder 1975). Snow usually covers the ground from mid-October until the end of April, and winters are long, dark, and cold. Pringle (this publication) describes weather conditions for the Grand Detour area of the SRL from 1968 to 1974.

Figure 1
Hook Lake (A) and Grand Detour (B) study areas, Slave River lowlands, NWT



The annual precipitation at the southeastern limit of the SRL, Fort Smith, averaged 33 cm (40% as snow) during 1943–72 and 47 cm during 1973–75 (Reynolds *et al.* 1978). The mean annual temperature was −3.5°C during 1941–70, with an annual average of 134 frost-free days; however, the consecutive number of frost-free days averaged only 64 (Reynolds *et al.* 1978). The growing season, based on 5.6°C, averaged 141 days in Fort Smith and 130 days in Fort Resolution (at the northern end of the SRL) for 1950–59 (Day 1972). Generally, precipitation and temperature are highly variable and, occasionally, extremely so.

4. Soils

Day and Leahey (1957) originally described nine soil series and four land types in the SRL and Day (1972) identified seven new soil series. Day (1972) rated about 18% of the soils in the survey area of 832 175 ha as belonging to class 3 in terms of agricultural capability, and 6% to class 4, both soils which have some limitations to agriculture but can produce cereal and forage crops; 58% as belonging to class 5, soils best suited for production of forage crops and pasture; 6% as belonging to class 6, soils best suited for native or unimproved pasture; and 9% as belonging to class 7, soils which cannot be used for arable agriculture or permanent pasture. The most commonly occurring soils are humic gleysols and gleysols that have developed under poorly drained conditions and together comprise 50% of the soils of the region. Regosols (33%) and brunisols (6%) are the next most common soils, but are weakly developed because of the cool dry climate and the youthful soil material (Day 1972). Pringle *et al.* (1975) reported that sodium, in amounts that could limit agricultural production, was present in several samples collected from the Hook Lake and Grand Detour study areas (Fig. 1).

5. Vegetation

The SRL are included in the Upper Mackenzie section of the boreal forest region described by Rowe (1972). White spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and trembling aspen (*P. tremuloides*) form the main forest cover on alluvial flats bordering the rivers. The drier sandy soils of the uplands, extending away from and above the flood plains, support populations of jack pine (*Pinus banksiana*), lodgepole pine (*P. contorta*), and trembling aspen, whereas black spruce (*Picea mariana*) and tamarack (*Larix laricina*) are prevalent on wet sites (Rowe 1972). Large expanses of open meadows, supporting sedge and grass communities, are interspersed in the forested lowland areas. Shrub communities dominated by willows (*Salix* spp.) are scattered throughout the meadows.

The vegetation of the SRL comprises three main types: meadow, shrubland, and forest (Day 1972). Reynolds *et al.* (1978) have described the wet and dry meadows in the Hook Lake study area. Sedges and grasses dominate the cover of the wet meadows: slough sedge (*Carex atherodes*), beaked sedge (*C. rostrata*), and water sedge (*C. aquatilis*) are the most common sedges; reed grasses (*Calamagrostis* spp.), whitetop grass (*Scholochloa festucacea*), and manna grasses (*Glyceria* spp.) are the most common grasses. The dry meadows are dominated by grasses and forbs: northern reed grass (*Calamagrostis inexpansa*) is the most common, followed by baltic rush (*Juncus balticus*). Less common grasses in dry meadows are alkali grass (*Puccinellia borealis*), slender wheatgrass (*Agropyron trachycaulum*), foxtail barley (*Hordeum jubatum*), rough bent (*Agrostis scabra*), and blue grasses (*Poa* spp.). The three most common sedges of dry meadows are fernald hay sedge (*Carex aenea*), windsedge (*C. foenea*), and slough sedge, although in general, sedges do not contribute significantly to the biomass of dry meadows. Common forbs are strawberry (*Fragaria virginiana*), cinquefoil (*Potentilla* spp.), American vetch (*Vicia americana*), Canada goldenrod (*Solidago canadensis*), aleppo avens (*Geum aleppicum*), veiny meadowrue (*Thalictrum venulosum*), and western dock (*Rumex occidentalis*) (Reynolds *et al.* 1978). The shrublands and forests are constantly encroaching on the meadow types, creating transition zones of mixed habitat types.

Seasonal distribution, group size and structure, and movements of bison herds

George W. Calef
Jack Van Camp

1. Abstract

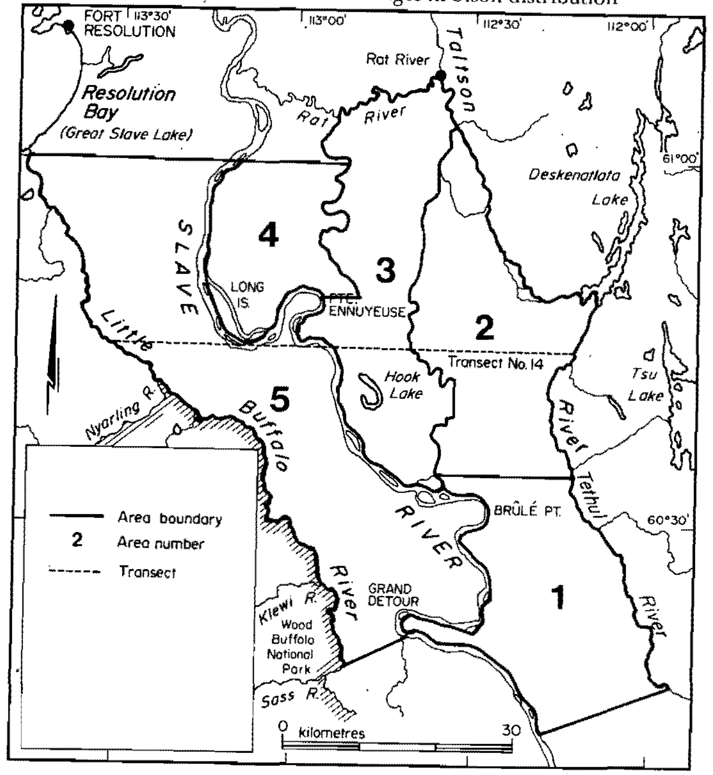
Information on seasonal distribution, group size and structure, and movement of bison in the Slave River lowlands (SRL) was collected between 1971 and 1978. Bison consistently used large, open prairies during May through July, the calving and post-calving period. Herds were largest during the post-calving period in June and July: more than 60% of the population occurred in herds of more than 100 animals at that time; usually, mature bulls formed their own groups, which reached maximum size then. Large post-calving aggregations in open habitat may have been a response to biting insects and predators. Cow–calf groups tended to disperse and decrease in size as bulls joined them during the rut in August and September. Calves were uniformly distributed in the population only during the rutting season. The trend toward smaller group size during the rut and asynchronous breeding distinguished bison of the SRL from other bison herds and may have been attributable to characteristics of the habitat and/or stress in the population. Variations in winter distribution were related to weather and possibly to stress caused by harassment by wolves and hunters.

2. Introduction

An understanding of the movement, group size and structure, and seasonal range use of bison is necessary for effective management of bison in the Slave River lowlands (SRL). Seasonal movement and group size vary from herd to herd. Roe (1970) and McHugh (1972) cited historical accounts of single herds containing millions of free-roaming plains bison. However, McHugh (1958), Fuller (1960), Meagher (1973), and Van Camp (1975) observed that bulls were most often found in groups of fewer than 10 individuals, and mixed groups rarely contained more than a few hundred individuals. McHugh (1958), Meagher (1973), and Lott (1974) reported that bison formed the largest herds at the peak of the rutting season, whereas Fuller (1960) observed the largest herds before the onset of the rut.

Roe (1970) suggested that plains bison moved in relation to habitat type rather than latitude as they left the prairies in summer for parkland in winter. Those migratory habits resulted in westward or northward movements in winter (instead of a typical north–south migration) depending on their location at the time. McHugh (1958) and Meagher (1973) concluded that bison in Yellowstone National Park moved from the wintering valleys to higher summer ranges in spring and reversed directions in fall in predictable altitudinal movements. In Wood Buffalo National Park (WBNP), 80% of the bison usually wintered in predictable wintering areas (Soper 1941, Fuller 1962, Stelfox and Kingsley 1976).

Figure 1
Areas used for analysis of seasonal changes in bison distribution



Meagher (1973) cited evidence of occasional mixing of subpopulations but believed that in most years, subpopulations, groups, and even individuals traditionally returned to the same wintering and breeding areas. Hewitt (1921) referred to distinct northern and southern subpopulations of wood bison in WBNP. Soper (1941) and Novakowski (1961, 1965) believed that the plains bison introduced to the park between 1925 and 1928 mixed extensively and hybridized with the resident wood bison in the area of the introduction; however, Banfield and Novakowski (1960) discovered an isolated herd of bison in a remote area in the northwest corner of WBNP that resembled pure wood bison.

This paper reports results of studies conducted between 1971 and 1978 to document seasonal distribution, group size and structure, and movements of bison in the SRL.

3. Methods

3.1. Seasonal distribution

We observed bison from the air during bison and wolf censuses (Van Camp and Calef, this publication; Van Camp, this publication) and anthrax surveys between 1971 and 1978 and recorded numbers and locations of bison on 1:250 000 topographic maps. We flew total coverage counts in early and late winter and used the results in the analysis of distribution. To describe group sizes and movements, we used data from counts made at other times of the year. Locations of individual animals and groups, estimated numbers, dates, times, and general weather conditions recorded during all surveys (aerial survey techniques are described in Van Camp and Calef, this publication) were grouped according to six seasons as follows: calving (1 April to 31 May), post-calving (1 June to 31 July), rutting (1 August to 30 September), post-rutting (1 October to 30 November), early winter (1 December to 31 January), and late winter (1 February to 31 March). We allocated observations from each season to one of five areas (Fig. 1) and compared the percentages of bison observed north and south of the middle of the range (transect 14, Fig. 1) and east and west of the Slave River, respectively, to detect changes in the north–south and east–west distributions of bison during different winters. Observations made during late winter, calving, and post-calving seasons served to delineate primary and secondary ranges.

3.2. Group size and structure

We categorized bison groups by size: 1–20, 21–100, and more than 100 animals. The number of bison associated with each size of group was calculated as a percentage of the total number of bison observed in each season. We distinguished bull groups from mixed groups between 1976 and 1978, calculated mean group size for the two group types, and made comparisons between seasons (*t*-test).

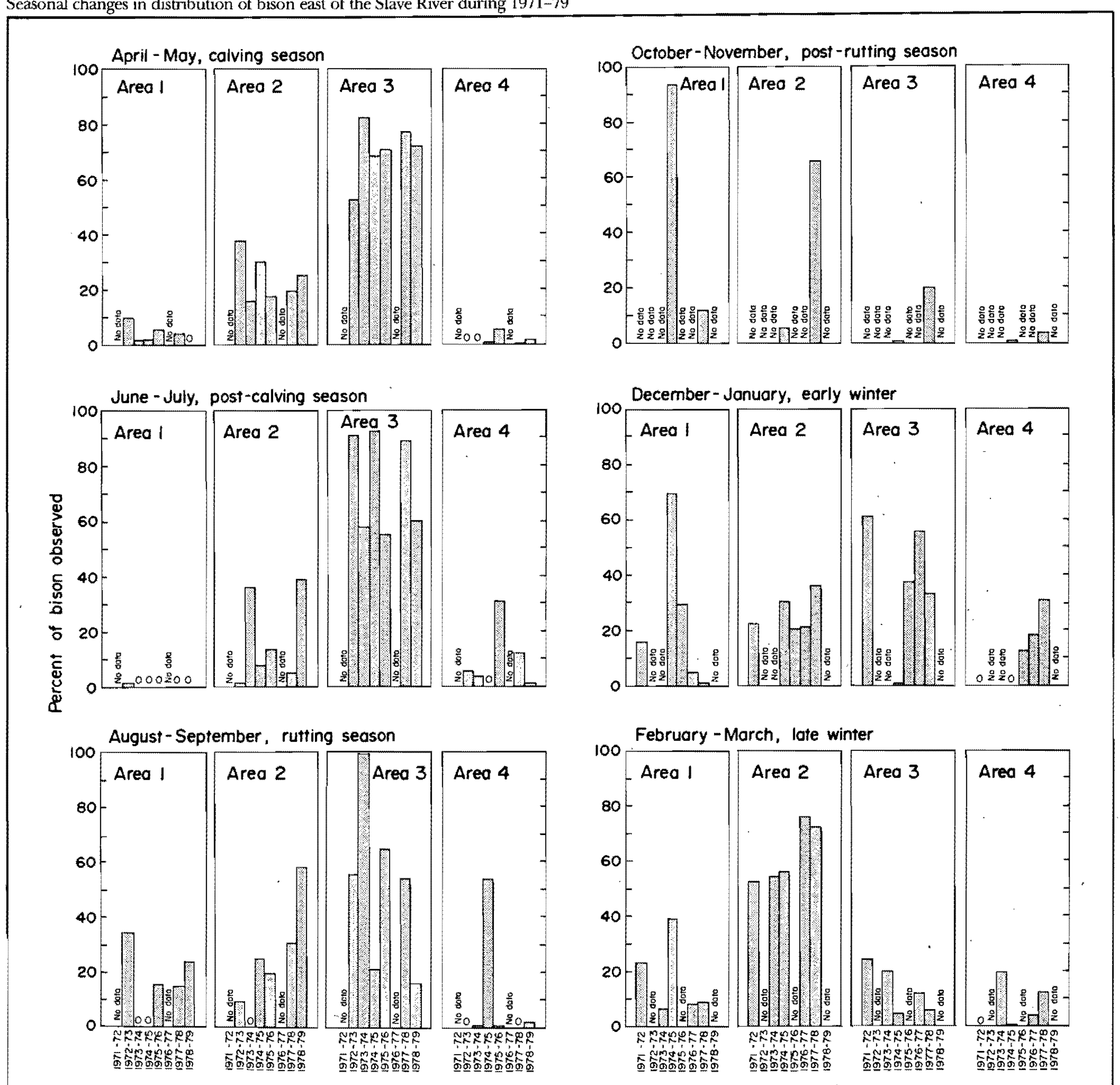
During each aerial census, we counted calves and total number of individuals in each mixed group. When four or more mixed groups were observed on one day, we calculated the total number of calves and individuals observed and then extrapolated the percentage of calves in mixed groups (by dividing total calves by total animals observed in all mixed groups). The expected number of calves for each mixed group could then be determined mathematically by multiplying the expected percentage (extrapolated) by the total group size observed. We tested the difference between the observed number of calves and the expected number of calves in each mixed group for each season using Chi-square analysis.

3.3. Marking of bison

To identify individuals and monitor herd movements we marked bison with neck collars. In June 1975 aircraft herded approximately 100 animals into corrals at Hook Lake for inoculation against anthrax. There we fitted 72 adult and subadult animals with coloured neck collars made from 20-cm wide strips of bright yellow, plastic-coated fibreglass, cut 115 cm long for cows and 140 cm long for bulls, and attached by fastening the ends with 0.5-cm nylon cord passed through holes cut in the fabric 4 cm from the edges of the collar. A combination of one number and one letter had been painted with Tuflex paint repeatedly along the length of the collar for field identification.

On 16 July 1975, we fitted eight adult male bison with red collars following immobilization with etorphine (M-99) administered by "Cap-Chur" rifle from a helicopter (Calef 1976).

Figure 2
Seasonal changes in distribution of bison east of the Slave River during 1971–79



4. Results

4.1. Seasonal distribution

Bison concentrated on the large prairies in the northern half of area 3 (Fig. 2) during the calving and post-calving periods. Figure 3 shows primary and secondary calving and post-calving ranges. During the rut, bison were most frequently observed in area 3 and along the Taltson River in area 2. Bison distribution was more uniform during the post-rut and early winter than during the other seasons. In late winter large numbers of bison congregated on the small prairies west of the Taltson River in area 2, but small groups also occurred in areas 1, 3, and 4. Primary and secondary ranges of bison in late winter are shown in Figure 4.

Prior to 1974–75, wintering bison were usually evenly distributed north and south of transect 14, a line that approximates the midpoint of the range lying east of the Slave River (Figs. 1 and 5). During winter 1974–75 most Hook Lake bison moved south of transect 14 and remained there until spring. From 1975 to 1977, the north–south winter distribution pattern of bison varied but, in 1977–78, it reverted to the earlier pattern.

The ratio of bison east and west of the Slave River remained nearly constant (approximately 4:1) between 1966 and 1977 (Table 1). In March 1978, 26% of the total SRL bison population was west of the river, corresponding to a population increase of approximately 30% west of the river and a decrease of 10% east of the river (see Van Camp and Calef, this publication). During March 1979, percentages of bison east and west of the river approximated the 1966–77 values.

Figure 3
Major calving and post-calving ranges of bison

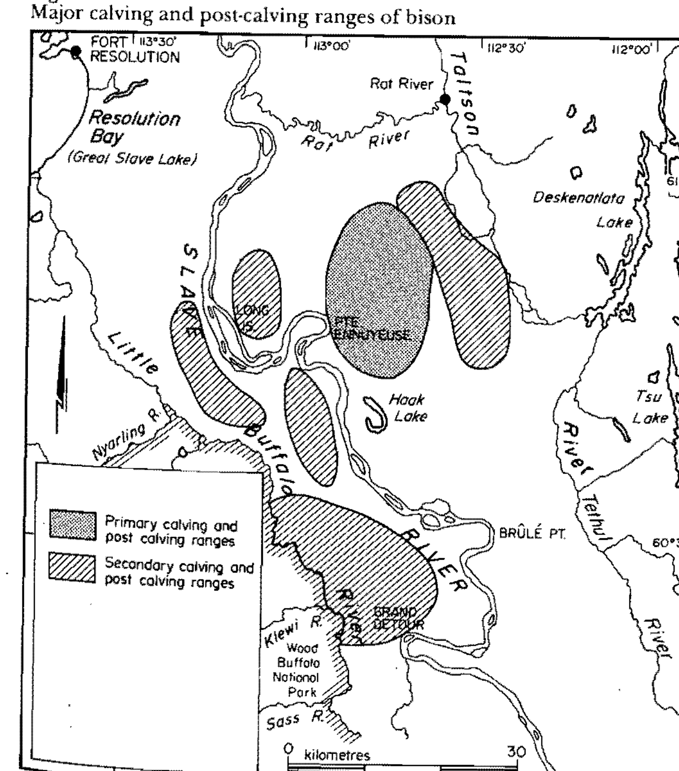


Figure 4
Major late winter ranges of bison

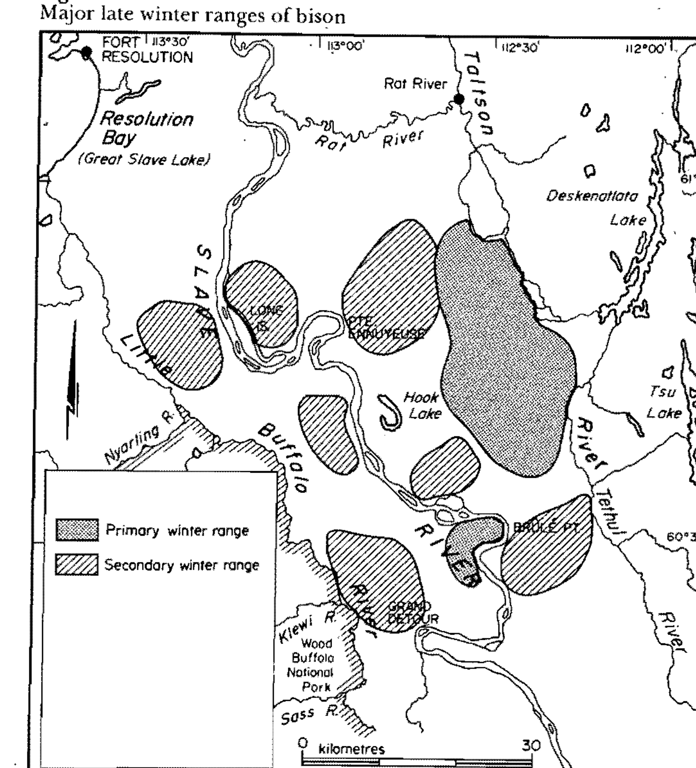


Table 1
Percentage of total bison in two subpopulations divided by the Slave River, March surveys, 1966–79

Year	% of total bison population: East of river	West of river
1966	82	18
1968	83	17
1971	84	16
1974	80	20
1975	81	19
1976	81	19
1977	80	20
1978	74	26
1979	81	19

Table 2
Seasonal changes in size of groups of bulls and mixed groups of bison, 1976–78

Season	Group type	Group size: Mean*	±	SE	Max.	Min.	Number of groups classified
Calving	Bull	3.9[a]	±	0.05	19	1	47
(1 Apr – 31 May)	Mixed	39.4[b]	±	4.1	180	5	59
Post-calving	Bull	4.2[a]	±	0.35	35	1	116
(1 Jun – 31 Jul)	Mixed	75.3[c]	±	6.0	250	7	75
Rut	Bull	1.3[d]	±	0.05	5	1	69
(1 Aug – 31 Sep)	Mixed	36.3[b]	±	2.3	88	6	58
Post-rut	Bull	2.1[e]	±	0.15	9	1	74
(1 Oct – 31 Nov)	Mixed	27.4[f]	±	2.6	94	1	65
Early winter	Bull	2.8[g]	±	0.25	9	1	80
(1 Dec – 31 Jan)	Mixed	37.6[b]	±	3.0	86	1	48
Late winter	Bull	2.7[eg]	±	0.15	12	1	228
(1 Feb – 31 Mar)	Mixed	37.3[b]	±	2.6	132	1	90

* Means followed by the same letter are not significantly different (p >0.05).

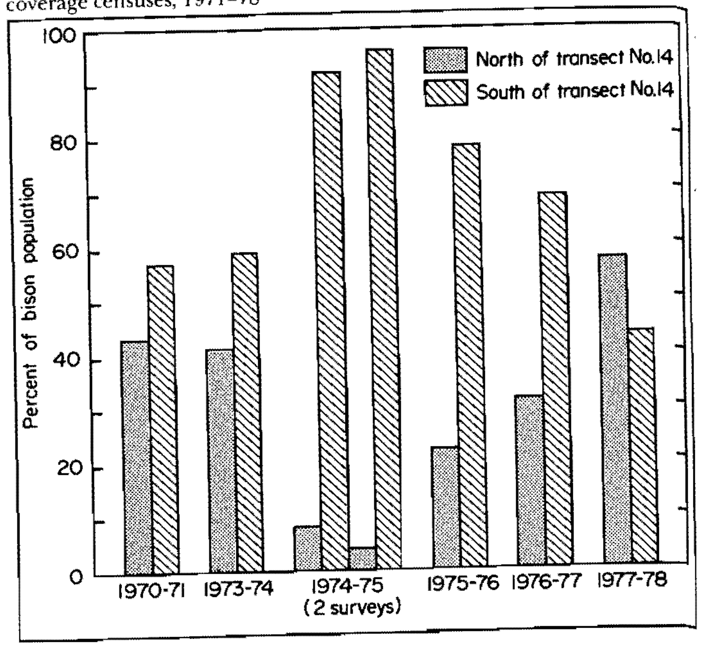
Table 3
Seasonal uniformity of distribution of bison calves in mixed groups, 1971–78

Season	No. mixed herds classified	Chi-square	Probability of uniform calf distribution
Calving	46	106.7	0.005
Post-calving	63	140.4	0.005
Rut	29	17.3	0.950
Post-rut	49	91.6	0.005
Early winter	44	56.6	0.100
Late winter	80	143.3	0.005

4.2. Seasonal changes in group size and structure

Bison were most often in large groups during the post-calving season (Fig. 6). These large group sizes occurred at the same time that bison frequented large prairies in the northern half of area 3 (Fig. 2). Bull groups reached a maximum mean size of 4.2 individuals during the post-calving period (Table 2). The largest bull group observed comprised 35 mature bulls. During the rut, the average bull group size decreased to 1.3. After the rut, bull group size gradually increased to an average of about three and remained constant during the winter (Table 2). The size of mixed groups followed the same trend as that of bull groups (Table 2). Late in the calving season, large groups began to form in the post-calving areas. Calef (1976) twice observed mixed herds of nearly 1000 animals during the post-calving season in 1975. We recorded a maximum mean group size of 75 during the post-calving season. Mixed herds tended to disperse as bull groups joined the mixed groups for the rut (Table 2) and by the time it ended, mixed groups were relatively small and widely scattered. This pattern continued through the post-rut so that mixed groups declined to the lowest mean size (27) of the year. By early winter, the mean size of mixed groups (37.6) had increased significantly (p <0.05)

Figure 5
North-south distribution of bison population during late winter total coverage censuses, 1971–78



and remained constant for the rest of the winter (Table 2).

During late July and early August, bison bulls on the SRL began mixing with the large post-calving groups of females and young. The post-calving grounds also served as a pre-rutting area where the normally scattered bull groups gathered prior to joining the mixed groups at the onset of the rut. During the rut, bison herds split into smaller groups, moved frequently, and selected smaller meadow and willow-shrub areas than they had earlier. They usually remained in the smaller meadow-shrub areas for the duration of the rut.

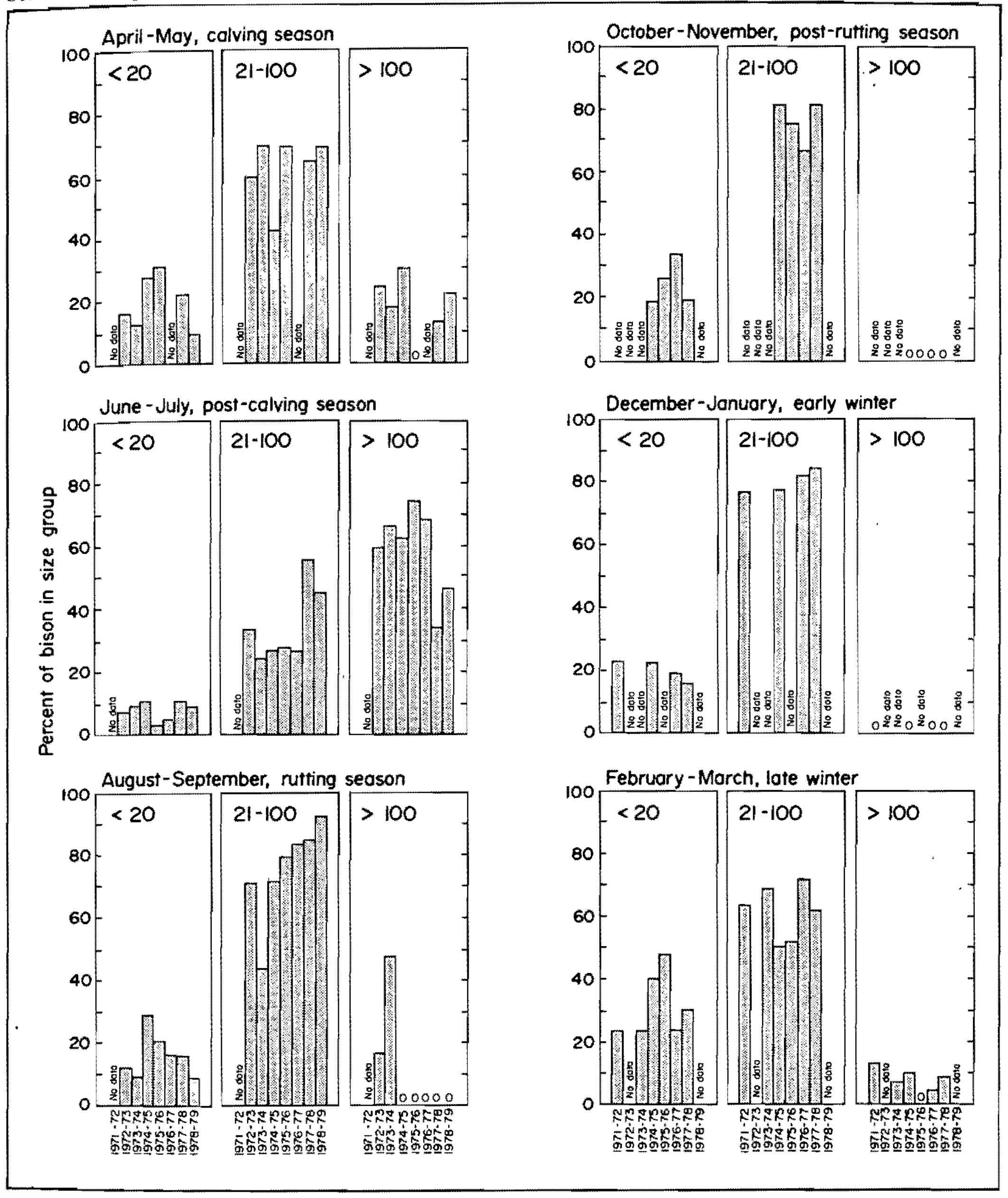
Only during the rutting season were calves distributed among mixed groups in a predictable fashion. In all other seasons, some of the mixed groups contained more calves than would be expected whereas other mixed groups contained fewer calves than would be expected (Table 3).

4.3. Movements of marked bison

Most of the bison marked with yellow collars retained them through summer and fall 1975. We observed collared animals from both air and ground throughout this period and found it more difficult to see bison collars than we had expected. Many collars became twisted, some reversed, and some were hidden by the long, dense hair of the neck, making it impossible to read numbers from aircraft. Red collars were even more difficult to see than yellow collars, and could barely be discerned from the air. Red collars were never observed more than 3 weeks after they were applied in July 1975.

Most yellow collars were lost by the end of winter 1976, but a few remained intact for up to 3 years through summer 1978. Collared bison were observed in nearly all parts of the range east of the Slave River except in the large system of prairies to the south in area 1 (Figs. 1 and 7). No bison collared at Hook Lake in 1975 was observed west of the Slave River.

Figure 6
Seasonal changes in the size of bison groups during 1971–79



5. **Discussion**

During most of the year mixed herds of bison were scattered throughout their range in groups of 20–60 animals. Mature bulls were occasionally solitary but were usually observed in groups of two to five individuals. This pattern changed during the post-calving, rutting, and late winter seasons. Group size increased two- to threefold during the post-calving season. Those large groups were most frequently seen in the northern half of area 3 (Figs. 1 and 2). The concentration of bison in large herds also coincided approximately with the insect season. The most frequently occupied post-calving ranges on the east side of the Slave River contained the most open habitats. Shackleton (1968) also observed that the largest groups of bison occupied the most open habitats in Elk Island National Park. Open habitats offer the greatest exposure to wind, and large post-calving concentrations of bison may be the result of animals moving to open areas to seek relief from insect harassment. However, insect avoidance does not explain the formation of large concentrations (similar to those during the post-calving season) in mid-May 1978 before the onset of the insect season. Also, those large concentrations dispersed during mid-July when horsefly (Tabanidae) activity was still intense. Social imperatives may also play a role in determining seasonal group size.

Post-calving aggregations may provide some protection against predation. Bison with young susceptible calves could reduce their vulnerability to wolves by concentrating in a relatively small area. The post-calving season for bison in the SRL coincided with the wolf denning season when wolves remain close to their whelping dens (Van Camp, this publication). Because only one wolf pack had a den in the northern half of area 3, by concentrating in that area the bison were exposed to predation from only one pack of wolves, whereas they would have been exposed to at least three or four packs if they had been scattered throughout the SRL.

Wolves concentrate their hunting efforts on the most vulnerable or conspicuous individuals in a group (Mech

1970; Peterson 1977; Van Camp, this publication). An individual calf is less conspicuous, and less likely to be the most vulnerable animal, in a group that contains other calves. Similarly, a male bison or a female without a calf will be less likely to be killed by wolves if it moves away from groups of females and young on which predators concentrate their hunting. Such segregation of females with young from males and non-breeding females is also observed among caribou and mountain sheep (D. Russell, pers. commun.; Geist and Petocz 1977). Selective pressures caused by predation may explain, in part, the large post-calving concentrations of bison as well as the uneven distribution of calves in mixed groups during all seasons except the rut.

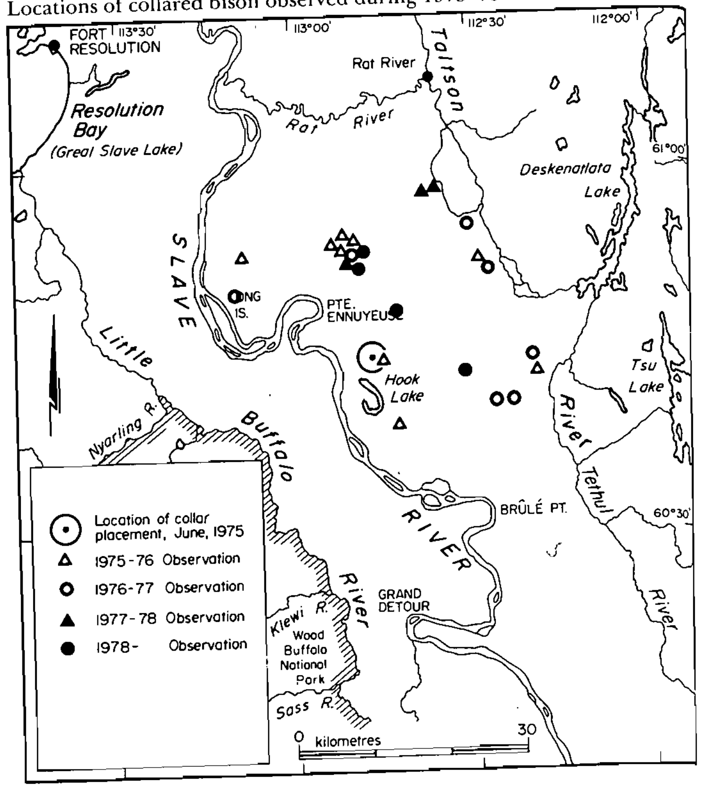
Breeding among bison in the SRL was not synchronous. Rutting behaviour was observed from late July through September. Calving commenced by mid-April and continued through mid-June. The formation of small dispersed rutting groups would allow bulls to monopolize a group of pre-oestrus and oestrus cows for an extended period of time. Such a strategy would select bulls with stamina rather than bulls with strength enough to defeat all challengers during a short rutting period. This breeding pattern contrasts with that reported for plains bison. Among plains bison, group size increases throughout the summer and reaches a maximum during the peak of the rut. In some years an entire herd may form one large rutting group (Lott 1974). Most plains bison cows in southern locations come into oestrus synchronously, and the majority of breeding occurs within 10 to 20 days (Haugen 1974, Lott 1974). Through a combination of fighting and display, dominant bulls can exclude subordinates from breeding (Lott 1974).

The difference between the breeding patterns of plains bison in southern regions and bison in the SRL may be related to differences in habitat and nutritional status. The interspersed woodland habitats of the SRL provide an abundance of cover that enables bison cows and newborn calves to hide from predators immediately following parturition. Synchronous calving presents predators with an overabundance of vulnerable prey for a short time, which is a definite advantage for open country animals but less so for woodland species. Breeding in small dispersed groups may also reflect poor condition in the population. Asynchronous breeding in dispersed groups of bison has been reported in two stressed populations, one in the SRL (Van Camp and Calef, this publication) and one on Catalina Island (Lott 1974). On Catalina Island, after an extended period of severe drought, plains bison bred in small dispersed groups with a single bull in each group (Lott 1974).

The evidence of equal distribution of calves among the mixed groups during the rut suggested that dry and nursing cows mixed more freely at that time than during any other season. Egerton (1962) suggested that the cow–calf relationship begins to weaken during the rut. The tending behaviour of the bulls and the intensity of the rut interfere with the usual behaviour of nursing females in banding together with their calves.

During the winters 1974–75 and 1975–76 most of the bison on the east side of the Slave River moved farther south and formed smaller groups than in other years. Bison arrived on their post-calving ranges later than usual in 1975 and did not use the same areas. Post-calving distribution and group size returned to the usual pattern during summer 1976. Group size in late winter returned to pre-1974 values during winter 1976–77 and north–south distribution returned to the normal pattern in 1977–78. These deviations in herd behaviour coincided with major population declines and lower rates of reproduction during 1974–77.

Figure 7
Locations of collared bison observed during 1975–78



Also, the number of sightings of wolves and the number of bison carcasses observed during late winter surveys increased for that period (Van Camp, this publication).

In November 1974, a snowstorm followed by freezing rain blanketed the northern half of the bison range east of the Slave River. The subsequent severe winter of 1974–75 may have caused the bison to abandon their normal winter ranges and fragment into smaller groups. If snow and ice conditions prevented the bison from foraging effectively, many bison would have become nutritionally stressed and would have been more vulnerable to wolf predation and disease.

In March 1978, an anomaly in the distribution of bison east and west of the Slave River was observed. East to west distribution of bison on the SRL was similar each year between 1966 and 1977. Calef's (1976) hypothesis of two separate subpopulations was supported by evidence that none of the bison that were marked with neck collars while on the east side of the Slave River were ever located on the west side. However, the subpopulation east of the river declined by approximately 50 individuals, whereas the subpopulation west of the river increased by approximately the same number in 1978. The ratio of bison observed west of the river during the 1978 survey was significantly higher than that observed during previous surveys. Whether bison crossed the Slave River could not be determined; however, in 1979 both subpopulations again declined and the east–west distribution ratio returned to the usual pre-1978 values (M. Jalkotzy, pers. commun.). The temporary increase in bison west of the river could have resulted from an immigration of bison from the northeast region of WBNP and their return to the park later that year.

Population dynamics of bison

Jack Van Camp
George W. Calef

1. Abstract

Bison populations in the Slave River lowlands declined from an estimated 1904 animals in March 1974 to an estimated 354 animals in April 1983. During that period, initial production of calves by mature cows and recruitment of yearlings were the poorest reported for bison in North America. A skewed adult sex ratio (32 adult bulls per 100 adult cows) and low numbers in the subadult cohorts (yearlings and subadult females and bulls comprised 6.8% of the total population in summer 1978) resulted in an unusually large proportion of adult females (55.7% of the total population in early summer). During 1978, the most productive year for the bison in the study period, fewer than 50% of mature cows produced calves and only 35% of mature cows had calves that survived to the end of the calving season (late June). During the period of decline from 1974 to 1979, initial calf production averaged 17.5% of total animals in the population and, from 1973 to 1979, recruitment of yearlings averaged 3.9% of total animals. Low reproductive rates, poor calf survival, and poor yearling recruitment can likely be attributed to a combination of factors, including hunting pressure and wolf predation (Van Camp, this publication), diseases (Broughton, this publication), loss of fertility because of old age, and stress caused by harassment from wolves and humans.

2. Introduction

The earliest record of bison in the Slave River lowlands (SRL) was supplied by Hearne (1795), who observed a bison hunt in the area south of Great Slave Lake and east of the Slave River in January 1772. Hewitt (1921) reviewed the early steps taken to protect the remaining herd after the extirpation of the northern bison from most of their historical range. Soper (1941) documented the transplant of plains bison between 1925 and 1928 to areas along the Slave River within Wood Buffalo National Park (WBNP) and the subsequent growth and range expansion of the resulting hybrid population.

Bison reinvaded the ranges east of the Slave River in the area north of Fort Smith during the 1940s. By 1949 it was estimated that about 200 animals wintered between the Slave and Taltson rivers (Fuller 1950). Novakowski (1957*a*, 1959) estimated 2643 bison in the SRL in 1957, but only 1300 in 1959. In 1961, an estimated 1450 bison occupied the area between the Little Buffalo and the Taltson rivers (Novakowski 1961). The bison population in the SRL was estimated at between 1300 and 2500 when anthrax outbreaks occurred between 1962 and 1964 (Choquette *et al.* 1972).

Officials in WBNP believed that mixing between bison in the north-east area of the park and those of the Hook Lake area on the east side of the Slave River occurred only occasionally. They theorized that the spread of anthrax could be contained by creating a "buffer zone" between those two groups of bison. Therefore, in 1964 and in 1965 an effort was made to kill all bison in the Grand Detour area on the west side of the Slave River between Little Buffalo River and Slave River. During November 1964 and March 1965, 522 bison were slaughtered in that area (Novakowski 1965; Choquette and Broughton 1967*b*), but within a few months a similar number of bison had moved into the depopulated area.

Between 1949 and 1961, four population estimates based on 25% coverage were made for the SRL bison herd (Fig. 1). Aerial surveys to estimate the number of bison in the SRL were made in 1966, 1968, and 1971 and, in each of the 10 consecutive years from 1974 to 1983, total count censuses were attempted (Williams 1966; Hall 1968; Rippin 1971; Baker 1974; Calef 1976; Van Camp 1978*a*, 1978*b*; Jalkotzy 1979; Hawley *et al.* 1980, 1982; R. Case, pers. commun.).

Data on calf production and survival were obtained during the 4-year period from 1975–76 to 1978–79 (Calef 1976; Van Camp 1978*a*, 1978*b*; Jalkotzy 1979). Recruitment of yearlings was estimated in 1968 (Hall 1968) and annually between 1972 and 1979 (Baker 1974; Calef 1976; Van Camp 1978*a*, 1978*b*; Jalkotzy 1979). During the calving and post-calving season of 1978, an effort was made to determine the sex–age composition of the herd.

This paper is a summary of the analyses of the data available to estimate population size, reproductive rates, recruitment rates, and sex–age composition of the SRL bison population.

3. Methods

The number of bison on the SRL was estimated from counts made from airplanes. Fuller (1950) and Novakowski (1957*a*, 1959, 1961) made total population estimates based on 25% coverage and extrapolation using sample results from partial coverage surveys flown in 1949, 1957, 1959, and 1961. Similar methods were used to determine each of those population estimates. Williams (1966) and Hall (1968) flew transects yielding 50% coverage. Rippin (1971) conducted the first total census at an altitude between 250 and 350 m above ground level (agl) using transects 3.2 km wide. Total censuses conducted in 1971 and from 1974 to 1979 were carried out using similar techniques and flight lines. In 1980, the intensity of search was increased by narrowing the transect width to 2.5 km and by increasing the number of transects from 29 to 41 (Hawley *et al.* 1980). Subsequent total censuses were made on transect lines established in 1980.

The survey crew consisted of pilot, recorder-navigator, and two observers. Each observer was responsible for reporting bison on his or her side of the aircraft. Pilot and recorder-navigator made observations on the line of flight, an area that cannot be covered by observers in the rear seats of the aircraft. Observers reported all bison to the recorder-navigator, who plotted their observations directly onto 1:250 000 topographical maps and standardized data sheets. The aircraft proceeded along designated flight lines (transects) but often circled large groups of bison until total counts and numbers of calves were obtained. Photographs were often taken as an aid to verify visual observations, but replicate counts were not conducted. Censuses were conducted in late winter and, if possible, after a fresh snowfall so that tracks would be visible.

In addition to the population counts, monthly calf surveys were conducted during 1975–76 to 1978–79 from either a Cessna 185 or a Bellanca Scout. Major prairies, bison trails, and known concentration areas were searched and bison observed were classified by sex and age. Large groups were circled, photographed, counted at regular census altitude, and counted again from approximately 160 m agl to determine the number of calves. Calves were also counted during aerial wolf surveys and ground segregation counts of bison. Visual counts were verified using photographs when possible. The percentage of calves was calculated by dividing total calves times 100 by total bison.

Various techniques were used to calculate the percentages of each sex and age class in the population because, from the air, only calves and mature bulls could be distinguished from other age classes. The percentage of bulls in late winter was calculated by dividing the number of bulls, times 100, by the total count during the late winter census. The bull percentage in summer was calculated by dividing the number of bulls observed during the late winter census, times 100, by the total estimated summer population (which was the sum of the late winter population estimate and the estimated number of new calves). Estimates of numbers in other sex and age classes were obtained by ground counts during the 1978 post-calving season.

Areas with concentrations of bison were located from the air and then searched on the ground. Observed bison were assigned to one of six age and sex categories (Table 1). All summer counts were made east of the Slave River in the Hook Lake area. An estimate of the percentages of mature cows, subadult females, subadult bulls, and yearlings was obtained by subtracting the summer aerial estimates for bulls and calves from 100%. All cows and subadults were assumed to be in mixed groups during early summer; so an estimate for each age class was calculated by eliminating bulls and calves from the mixed group sample. A percentage for each sex–age class in the remaining mixed group sample was determined from ground count data and then multiplied by the percentage of all animals in the remaining sex–age classes. For example, if there were 20% calves and 20% bulls, then 60% of the herd would be in the remaining sex–age classes. If mature cows represented 80% of the mixed herd total after bulls and calves were eliminated from the sample, then mature cows represented $0.8 \times 0.6 = 0.48 = 48\%$ of the total herd. Similarly, percentages for each of the subadult female, subadult male, and yearling age classes were calculated.

Table 1
Criteria for age and sex segregation of bison

Calf	Red coat, horns undeveloped, very small body size.
Yearling	Small body size, straight horns.
Subadult female	Small diameter horns, not fully developed, no penis tuft, body size small to average.
Mature female	Small diameter horns fully curved and recurved, small head and front quarters, no penis tuft, body size average.
Subadult male	Large diameter horns not fully curved, large head, penis tuft, body size average to large.
Adult male	Large diameter horns, fully curved but not recurved, massive head and front quarters, penis tuft, large body size.

4. Results

4.1. Population estimates

Bison numbers in the SRL have been declining since 1971 (Fig. 1). The size of bison populations on the east and west sides of the Slave River have varied independently and are considered to be subpopulations (Calef 1976). Between 1974 and 1982, the subpopulation east of the Slave River declined at a rate between 6.5 and 33% per year (mean = 17.5% per year). During this period, the subpopulation west of the Slave River was relatively stable, fluctuating around a mean of approximately 200 animals (Fig. 1). The value for the 1957 partial coverage survey data (total population estimate of 2643 extrapolated from an actual count of 664) from Novakowski (1957*a*) appears to be anomalous; however, the survey method is comparable to other partial coverage surveys conducted in 1949, 1959, and 1961.

4.2. Production and survival of calves

Both initial calf production and survival of calves were low. Most of the calves born in spring 1975 were lost before winter. In May 1975, calves constituted 15% of the population but by March 1976, calves accounted for less than 2% of the herd (Fig. 2). During spring 1976, the calf crop was 18%, and many calves survived through that summer and autumn. However, by January 1977, calves represented only about 10% of the herd, and this value dropped to 5.6% by March. During early summer 1977, the calf crop was only 15% and calf survival was poor during the rest of the summer. By December, calves represented only about 6% of the entire herd (Fig. 2). Between December 1977 and March 1978, the percentage of calves in the population decreased to approximately 5%. The May 1978 calf crop of 22% was the highest initial calf production recorded for the SRL. By September 1978, calves represented approximately 15% of the total population. In December 1978, calves accounted for approximately 11% of the population, but by March 1979 the percentage of calves had dropped to about 5.5% (Jalkotzy 1979).

Calf survival was two to three times greater in the subpopulation on the west side of the Slave River in late winter 1977–78. Calf survival was approximately equal in the bison herds on both sides of the Slave River for 1978–79. During the 7-year period 1973–79, the percentage of the total herd in the yearling age class (indicative of calf recruitment) ranged between 1.5 and 5.6 (mean = 3.9%) (Table 2).

Table 2
Recruitment of bison calves into the yearling age class, 1968–79

Year	Yearlings as % of total herd	Estimated number yearlings recruited‡
1968*	11.4	169
1972†	10.0	200§
1973†	1.7	34§
1974†	4.4	84
1975*	3.1	39
1976*	1.5	14
1977*	5.6	42
1978*	5.4	41
1979*	5.5	30
Mean 1973–79	3.9	40

* Data collected during March census surveys each year.
† Data on number of yearlings among animals handled during anthrax control roundup in July of each year.
‡ Calculated by multiplying the estimated total population (data from Fig. 1) by the percentage of yearlings.
§ Assumes total population of 2000.

4.3. Bison population structure in summer 1978

In March 1978, 752 bison were counted, of which 165 (21.9%) were identified as mature bulls. The total summer population in June 1978 was estimated at 936, including an estimated 184 calves (19.7%) (Fig. 2). Therefore, 165 mature bulls would have represented approximately 17.6% of the early summer population (Table 3).

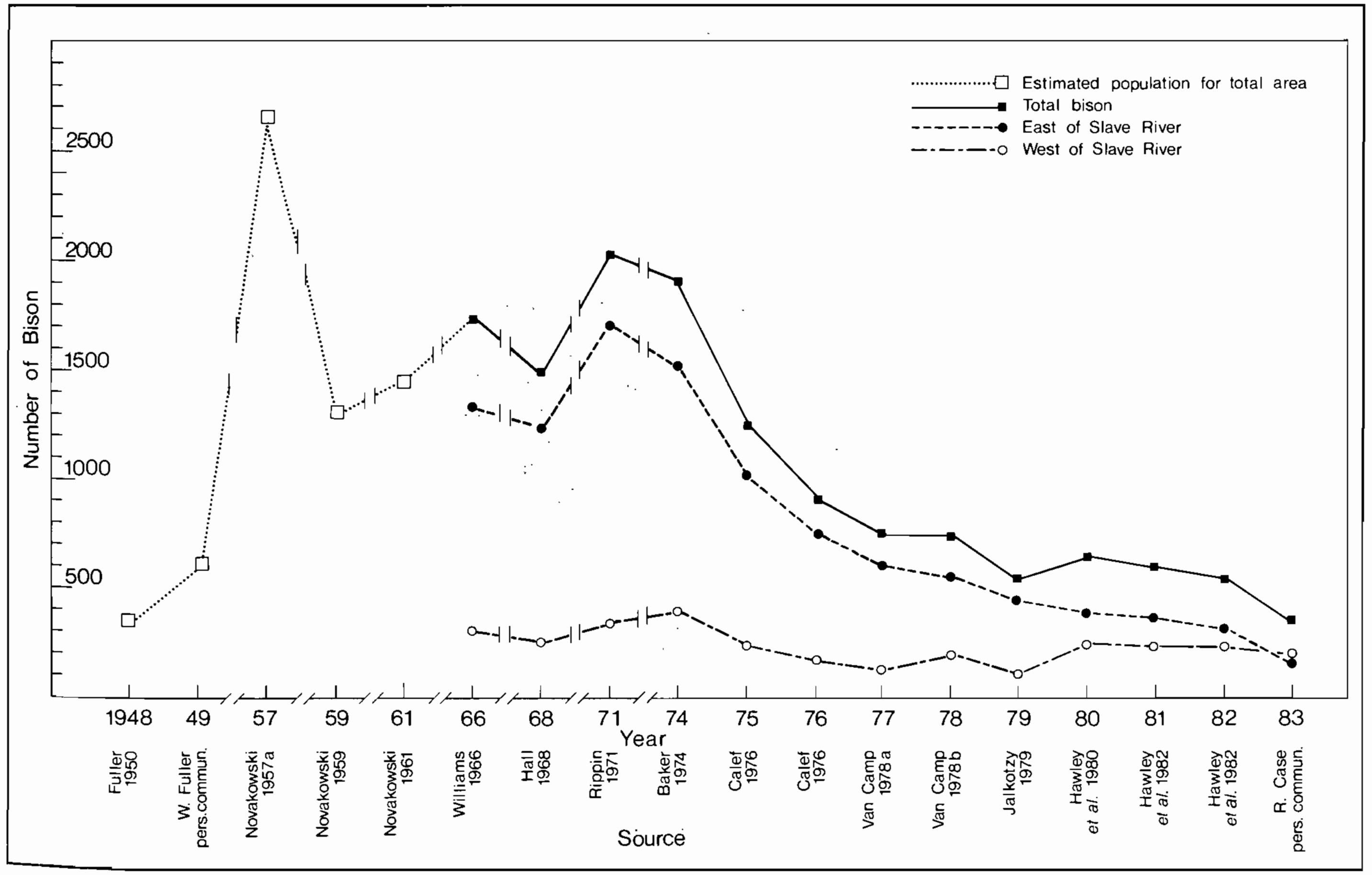
The aerial calf count at the end of May 1978 resulted in an estimate of 22% calves in the herd. By the end of June, calves represented 19.7% and adult bulls represented 17.6% of the population (Table 3). Of the remaining sex and age classes, the following percentages were observed from a sample of 536 animals during June and July: mature cows 89%, subadult cows 1%, subadult bulls 4%, and yearlings 6%. If it is assumed that this sample was representative of all herds in the SRL, then mature cows represented 55.7% of the entire population, subadult females 0.7%, and subadult bulls 2.4% (Table 3). If the 41 yearlings that were counted in March 1978 all survived the winter, then yearlings would have represented 4.4% of the early summer population in 1978. The ground classification yielded an independent estimate of 3.7% yearlings.

5. Discussion

5.1. Population trend

The precision and accuracy of bison population estimates prior to 1971 are questionable because of the incomplete coverage of the surveys, which necessitated extrapolation of the total estimate from sample data, and because of the clumped distribution pattern of bison. During the partial coverage survey in 1957, a large proportion of the population actually may have been counted, thereby yielding an erroneously high population estimate. We believe the 1957 data are anomalous for that or other unknown reasons and that the population continuously increased from 1948 through the mid-1960s. Between 1971 and 1975, a major decline was recorded (Fig. 1): approximately 33% of the herd east of the Slave River were lost during the severe winter of 1974–75. Killing of bison by wolves and humans also increased during 1971–75 (Van Camp, this publication). The rate of decline lessened after the major loss in 1974–75, but the population continued to decline through 1983.

Figure 1
Slave River lowland bison population for 1948–83 (annual surveys in 1971 and from 1974 to 1979 inclusive were flown along identical flight lines)



5.2. Production and survival of calves

The reproductive success of the SRL bison was poor compared to that observed for wood bison in the Mackenzie Bison Sanctuary (MBS) (Reynolds and Hawley, *Introduction*, this publication). During 1974–79, initial calf production in the SRL averaged 17.5% of the total herd. It reached a peak of 22% in late May 1978, but could have been as high as 25% because some calves may have already been lost. Calef (1984) reported calf production rates in the MBS ranging between 20.7 and 22.3% of the total early summer population. Although the estimates of calf production in the SRL appear to be only slightly lower, on average, than those of the MBS (17.5% vs 21.7%), expression of calf production as a percentage of the total population can be misleading if sex and age distribution are not considered. The MBS bison are assumed to have an equal sex ratio (Calef 1984). The SRL bison have a skewed adult sex ratio (32 bulls:100 mature cows), due in part to trophy hunting pressure and greater susceptibility of mature bulls to anthrax (Stephenson 1979). Assuming a 1:1 sex ratio, Calef (1984) calculated that the exponential rate of increase observed in the MBS population would be achieved if 90% of the mature cows produced one calf per year. In intensively managed plains bison herds, 90–100% of mature cows produce calves every year (Haugen 1974, Lott 1974, Van Camp 1975). Fuller (1962) reported that wild bison produced two calves per three cows in WBNP. In the SRL, 55.7% of the total population was producing an initial calf crop that averaged 17.5%. Thus, in 1978, the year with the highest calving rate during the study period, only about half of the mature cows produced calves. However, by early July, only one-third of the cows still had a calf.

Also, calf survival was poor on the SRL during other seasons. The season of greatest mortality varied from year to year (Fig. 2). In 1975–76 and 1977–78 most calves died in summer, whereas in 1976–77 and 1978–79 most calves died in winter.

Yearling recruitment in the SRL herd was poor compared with recruitment in the MBS. In the MBS population, probably 95% of the calves survived (Calef 1984), compared with less than 25% in the SRL. Recruitment of yearlings in the SRL in late winter ranged between 1.7 and 5.6% (mean = 3.9%) of the total population from 1973 to 1979 (Table 2). The estimated proportion of yearlings in the early summer population in 1978 was 4.4%, based on the number of yearlings counted in March 1978. In summer 1978, yearlings represented 3.7% of the total population observed during classification counts done on the ground. Thus, those two independent estimates of yearling recruitment in addition to the small number of subadults identified support the belief that poor calf survival in the SRL bison population has occurred for several years. Only 7 of 100 mature cows in the SRL produced calves that survived to enter the yearling age class in 1978 (Table 3). In contrast, nearly every mature wood bison cow in the MBS must have produced a calf every year and most calves must have survived in order to sustain the growth rate recorded (Van Camp 1978*c*, Calef 1984).

Several factors have likely contributed to the poor productivity of the SRL bison. The incidence of brucellosis and tuberculosis in the population is high (Broughton, this publication). In cattle, brucellosis causes sterility and loss of calves through abortion (Meagher 1973, Choquette *et al.* 1978). The effects may be similar in bison. Also, tuberculosis adversely affects reproductive performance in cattle and most likely has the same effect in bison. The quality of habitat in critical winter and calving ranges may have deteriorated as a result of the absence of fire and subsequent accumulation of plant litter in the drier prairies for many years (Jalkotzy and Van Camp 1977). Harassment by aircraft, wolves, and hunters may also have contributed to nutritional stress during critical seasons (Geist 1971*a*, 1971*b*). There was little recruitment to the SRL bison population during the period of decline from 1973 to 1979; therefore, older cows were not being replaced by younger females. As the age structure of the SRL population shifted to older animals, overall fecundity may have dropped, which could have contributed to poor productivity. Insufficient data are available to assess the relative importance of each of those variables independently, all of which could have contributed to the observed decline.

Figure 2
Number of calves as a percentage of total bison observed from 1975 to 1979

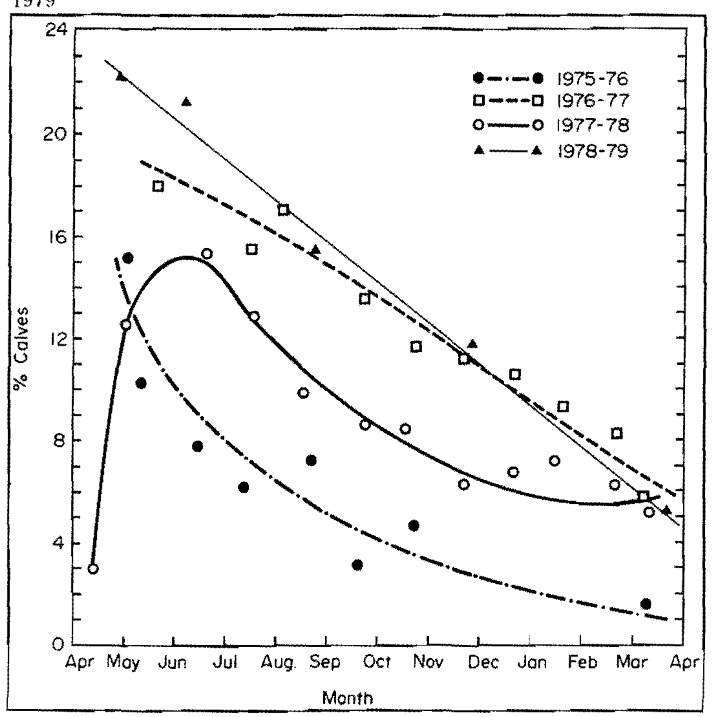


Table 3
Early summer population structure of bison in 1978

	Sex and age class					
	Calves	Yearlings	Subadult females	Subadult males	Mature females	Adult males
Percent of population	19.7	3.7	0.7	2.4	55.7	17.6
No. in class if population = 936	184	35	7	22	521	165
Ratio of each sex-age class per 100 mature cows	35	7	1	4	—	32

Predation on bison

Jack Van Camp

1. Abstract

During winter 1976–77, between 64 and 76 wolves were estimated to reside on the bison ranges of the Slave River lowlands (SRL), an area of approximately 4000 km^2. Movements of wolves in three of four radio-marked packs overlapped continuously for a minimum of 6 weeks during late winter 1977 in an area where bison were concentrated, but did not overlap during the denning season.

Bison was the most important of six major prey types eaten by wolves on the SRL and represented 88% of prey weight of wolf diets during the period of snow cover (8 November 1976 to 15 April 1977). At other times of the year, bison continued to be the most important prey type of two wolf packs whose denning territories included bison post-calving concentrations, but in two other packs, primarily small prey was consumed during the denning season.

Based on estimates for 22 weeks of winter, between 8 November 1976 and 15 April 1977, wolf predation in 1976–77 accounted for about 31% of the adult and subadult mortality and approximately 27% of the calf mortality. Hunting accounted for an additional 39% mortality and when combined with wolf predation, these two factors accounted for at least 70% of the adults and subadults lost that year.

During the winters of 1977–79, a wolf control program removed 72 wolves from the SRL, but the bison population continued to decrease. Wolf predation and human hunting were major factors contributing to the decline of the SRL bison population and appeared to be additive rather than compensatory mortality.

2. Introduction

Seton (1911) concluded that overhunting, rather than wolf (*Canis lupus*) predation, was the cause of the virtual absence of bison from suitable habitat near Fort Smith, Northwest Territories (NWT). Soper (1941) reported that bison were increasing and expanding their range during the early 1930s in Wood Buffalo National Park (WBNP). Soper (1941, 1945) travelled extensively on bison ranges in WBNP and communicated widely with a variety of interested people about bison and wolf interactions, but few data were reported. Soper (1941) recognized that wolves were a predator on bison but did not believe they were a serious threat to the expanding population. However, by the mid-1940s, he had reversed his opinion and concluded that wolf predation was keeping the bison population in WBNP below the limits of their habitat. Soper (1945) recommended a wolf control program if an increase in the bison herds was desired or if hunting of bison was to continue. Following this recommendation, wolf control programs were instituted sporadically in the Wood Buffalo region (Fuller and Novakowski 1955).

Fuller (1962), after examining 95 stomachs from poisoned wolves and 63 wolf scats, concluded that bison formed the major portion of the diet of wolves in WBNP. Fuller (1960, 1962) also reviewed 11 case histories of wolf–bison interactions and presented evidence of repeated attacks, long distance chases, and wounding. However, he believed that wolves selected young, handicapped, and aged animals that he considered a biological surplus. Wolf predation on bison in WBNP during the early 1950s was not "detrimental to general herd welfare" (Fuller 1962). Sporadic wolf control programs, bison roundups, and slaughters of bison to control disease and to supply meat locally were management practices that continued throughout the 1950s until the mid-1960s (Mitchell 1976). In the NWT between March 1965 and March 1975, a $40 bounty was paid on each wolf killed on bison ranges outside the park (Heard 1983). In spite of wolf poisoning programs, Mitchell (1976) concluded that bison in WBNP had never approached the estimated carrying capacity based on available habitat within the park.

The Slave River Preserve protected bison on the Slave River lowlands (SRL) until 1955, after which time resident hunting began. Two licensed outfitters operated in the SRL from 1959 to 1961, but hunting was closed in 1962 when the first known anthrax outbreak occurred.

The last abattoir slaughter of bison in WBNP was conducted in 1967 (Mitchell 1976). It was soon thereafter that the attention of native hunters from Fort Smith and Fort Resolution focused on the bison herds ranging in the SRL outside park boundaries. Resident hunting was reinstated in the SRL in 1968, and an outfitter was licensed to guide non-resident hunters in 1970. Bison became an important economic resource as well as a community symbol in Fort Smith and Fort Resolution. In 1973 and 1974, NWT game officials noted evidence of poor recruitment in the SRL bison population (Van Camp and Calef, this publication). In November 1974, a snowstorm followed by freezing rain forced the bison of the Hook Lake area to winter on ranges to the south of those normally used (Calef and Van Camp, this publication). That may have led to the high mortality of bison during that winter. Calef (1976) observed a continued decline in the SRL bison population and coincidentally noted evidence of an increase in the wolf population and increased signs of wolf predation during winter 1975–76. Wolves and evidence of wolf predation on bison were frequently found in the SRL from 1975 through 1977. Local residents became concerned that wolf predation was causing the observed decline and that their access to the bison would be stopped if the decline continued. In 1977, all hunting of bison, except for holders of the General Hunting Licence (GHL), was forbidden and the regular season was closed. Many opinions were offered but few data existed on wolf-bison relationships. The public persuaded the Government of the NWT to begin wolf studies.

By means of aircraft and telemetry systems, many recent studies have examined wolf–ungulate relationships at the population level (Mech 1966, 1970, 1977; Jordan *et al.* 1967; Kolenosky and Johnston 1967; Pimlott *et al.* 1969; Kolenosky 1972; Wolfe and Allen 1973; Van Ballenberghe *et al.* 1975; Haber 1977; Mech and Karns 1977; Peterson 1977; Stephenson and Van Ballenberghe 1978; Carbyn 1980, 1983). A predictive model has been developed and tested for wolf–ungulate systems in Alaska (Gasaway *et al.* 1983). Most of those studies have been carried out in areas of high density wolf populations where the primary prey has been white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), or elk (*Cervus elaphus*). The predator–prey relationships between wolves and gregarious species like caribou (*Rangifer tarandus*) and bison are less well known (Crisler 1956; Kuyt 1972; Parker 1972, 1973; Miller and Broughton 1974; Gasaway *et al.* 1983).

This report presents population data obtained from studies on wolves and bison that occupy ranges in the SRL and discusses the contribution of predation by wolves and human hunting to the decline in the SRL bison population.

3. Methods

3.1. Capture and radio collaring

Leg-hold traps (sizes #4 and #14) and wire neck snares (Kolenosky and Johnston 1967, Mech 1974) were used to capture wolves alive on the SRL during winter 1976–77. In March 1977, wolves were immobilized with 80 mg Sernalyn and 60 mg Sparine delivered by 3-mL darts fired from a helicopter using a "Cap-chur" rifle with low power charges. Wolves were located from a spotter airplane by checking known kill sites, finding bison herds, locating wolf trails, searching major prairies, and following winter roads and bison trails. When wolves were found, the spotter airplane guided the helicopter to them. One wolf was singled out and pursued by the helicopter until it was hit with a dart.

Once immobilized, wolves were measured, weighed, and fitted with collars made of machine belting carrying radio transmitters that operated in the frequency range of 150.000 MHz to 152.000 MHz (AVM Instrument Company, Champaign, Illinois). Collars were fastened with two locking nuts and the threads on the bolt ends were crushed to prevent loss of the nuts. Radio-collared wolves were located by means of a portable receiver connected to twin directional yagi antennae mounted on the spotter airplane.

3.2. Tracking

Relocation flights were flown one to three times per week when weather permitted (minimum ceiling 1000 m, visibility 7.5 km). The aircraft circled at 1000–2000 m above ground level (agl) until a radio signal was detected, and then an attempt was made to pinpoint the signal. Once in the vicinity of the signal, the aircraft circled at 150–200 m agl in search of wolves and signs of predation. Locations of radio signals, date, habitat, number and colour of wolves sighted, predominant behaviour, and observations of prey in the area were recorded for each sighting.

3.3. Territorial determinations and population estimates

Radio locations for each collared wolf were transferred to mylar map overlays. The most dispersed locations for wolves that were members of the same pack were connected by lines to determine home range of the pack. Home range size was measured by planimeter.

During winter 1976–77, the wolf population was estimated by summing the number of individuals in packs that contained individuals marked with radio transmitters. The density of wolves was determined by dividing the known number of individuals by the size of the area in which collared animals were travelling. The mean density of wolves within the home ranges of known packs ($N = 4$) was assumed to represent the density for the entire SRL. A factor of 10% was added to account for wolves that were not members of radio-equipped packs (Mech 1973).

In winter 1977–78, wolf tracks in the snow were counted during bison census surveys (Calef and Van Camp, this publication) and during 50 h of aerial searching for wolves in late March 1978. Those observations were related to the territories that had been mapped based on data from the previous year. The maximum number of animals observed or the maximum number of tracks counted was assumed to equal total pack size. Density was again calculated and extrapolated to include the entire SRL bison range. Because of the overlapping movements of wolves observed in winter 1976–77, the track-counting technique was considered less precise and less accurate than estimates obtained by relocating radio-collared individuals.

3.4. Evidence of wolf predation

It was assumed that wolves had killed bison if one or a combination of the following factors could be identified: hunters could be eliminated as a possible cause of death, wolf signs were abundant in the area surrounding the kill, tracks indicated that the dead bison had been travelling with other bison, the remains were fairly fresh and not frozen, or the carcass bore signs of severe wounding before death. Wolves were not deemed responsible for the kill if hunter tracks were evident at the kill site, if anthrax was active in the area, if the remains were obviously old, or if evidence suggested that the remains had been dug out and transported. Intact long bones of killed bison were examined for evidence of marrow fat depletion. Colour and consistency of the marrow were recorded.

3.5. Sex, age, and number of killed bison

Sex and age of wolf-killed bison were determined by examination of carcasses. Calf skulls and long bones were easily identified by their size. Subadults, cows, and bulls were segregated according to horn development and morphology (Van Camp and Calef, this publication). When possible, horn rings were counted and used to estimate age.

During 1968–75, the estimate of hunter-killed bison was based on actual kills reported by hunters and is assumed to be a minimum. Hunters reported bison killed anywhere in the NWT. Some were taken along the borders of WBNP but the majority were taken from the Hook Lake, Little Buffalo River, and Grand Detour areas on the SRL. During 1976–79, the number of bison killed by GHL holders was estimated by combining the number of bison kills observed in the field with those reported to wildlife offices in Fort Smith and Fort Resolution. Potential overlap was eliminated. Estimates of wounding loss were not included.

3.6. Wolf food habits

Wolf scats were collected throughout the year to determine food habits. Only scats greater than 2.5 cm in diameter were collected unless they were located near den sites. Small scats taken near known wolf dens were labelled as pup scats and included in the sample. Small scats located away from den sites were not sampled to avoid potential overlap with scats of coyote (*Canis latrans*) and red fox (*Vulpes vulpes*). Collection date and location were recorded for all samples. A. Kennedy, Canadian Wildlife Service, Edmonton, analysed the wolf scats to identify prey species according to techniques described by Kennedy and Carbyn (1981). The frequency of occurrence of major prey species in scat samples was converted to a relative percentage of prey weight in the diet sample using the regression equation method of Floyd *et al.* (1978). Several minor prey types were also identified in the scat samples; however, those were not included in the analysis of prey importance.

Scat samples collected during the period of snow cover (1 November 1976 to 31 March 1977) were kept separate from those collected during the snow-free period (15 April to 30 October 1977) so that comparisons of food habits between the two periods could be made. Fresh scats collected in 1977 during the snow-free period were also analysed according to the pack territories in which they were collected. Adult and pup scats collected from the Taltson River, Hanging Ice, and Hook Lake packs were taken at active den sites. The den site of the North Prairie pack was not located but fresh scats were collected from the territory of this pack during the snow-free period. The percentages of food items occurring in pup scats did not differ significantly from those occurring in adult scats; therefore, pup and adult scat samples were combined for the analysis.

3.7. Wolf control

An area of approximately 5600 km^2, including and surrounding the SRL, was designated as a wolf control area (Fig. 1) and a program was implemented to remove wolves. Between 15 November 1977 and 31 March 1978, trappers working in the area were offered an incentive of $300 for the return of each wolf carcass taken from the control area. An additional $25 was offered for the return of any radio collar obtained from a wolf. After 15 March 1978, any wolves that remained in the control area and could be located were shot from a helicopter using a shotgun. Wolf control was undertaken again during winter 1978–79, with the same trapper incentives.

4. Results

4.1. Radiotelemetry

During fall and winter 1976–77, 16 wolves were captured: one in a #14 trap set at a hunter-killed bison carcass, two in neck snares set on wolf trails, and 10 by immobilizing drugs. In addition, a 50-kg male wolf died of an apparent drug overdose and two mature female wolves died in neck snares. Thirteen wolves were fitted with radio transmitters.

Between November 1976 and December 1977, 351 radio locations were obtained. Seven additional radio locations were obtained during August 1978 from a wolf that had been collared in WBNP but had moved to the North Prairie area during the summer (S. Oosenbrug, pers. commun.).

The radio-collared wolves were members of four packs; four belonged to each of the North Prairie, Taltson River, and Hanging Ice packs, and one to the Hook Lake pack. The territories of each pack were drawn on a map using radio location data from the collared wolves (Fig. 2). Radio contact with the North Prairie pack lasted until May 1977. One radio was recovered from a yearling male after he was found dead in March 1977. Radio contact with the Taltson River pack was lost after 28 August 1977. The radio collar of a breeding female from that pack was recovered a

Figure 1
Location of the wolf control area

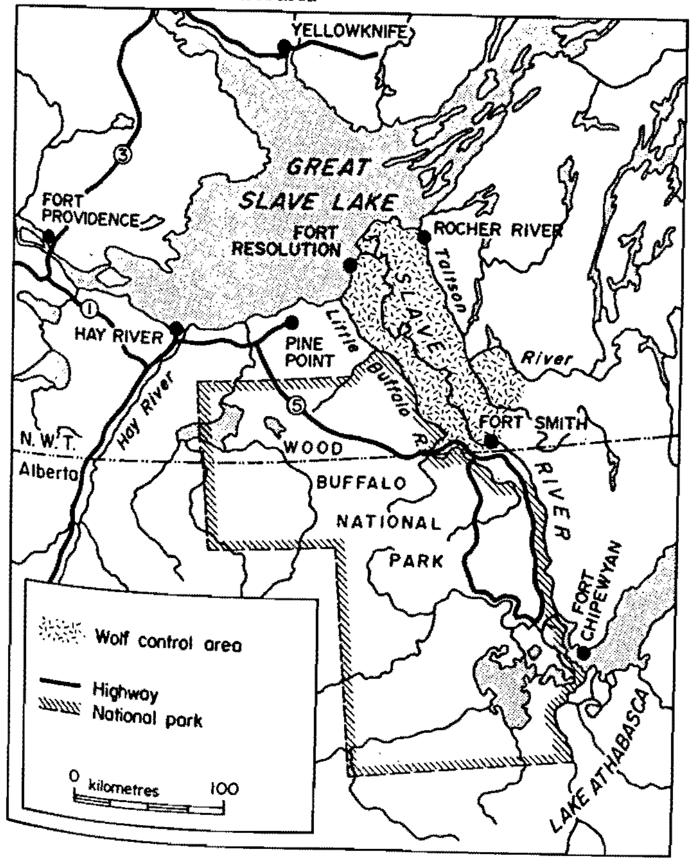


Figure 2
Wolf pack home ranges determined by radio locations of marked pack members

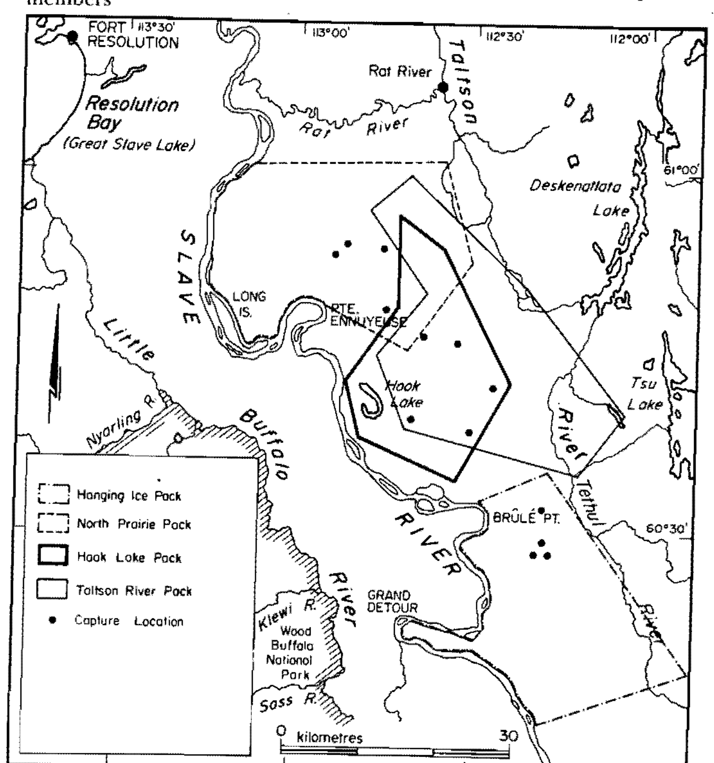


Figure 3
Overlapping home ranges of three wolf packs determined by radio locations of marked pack members and locations of bison carcasses between 3 March and 15 April 1977

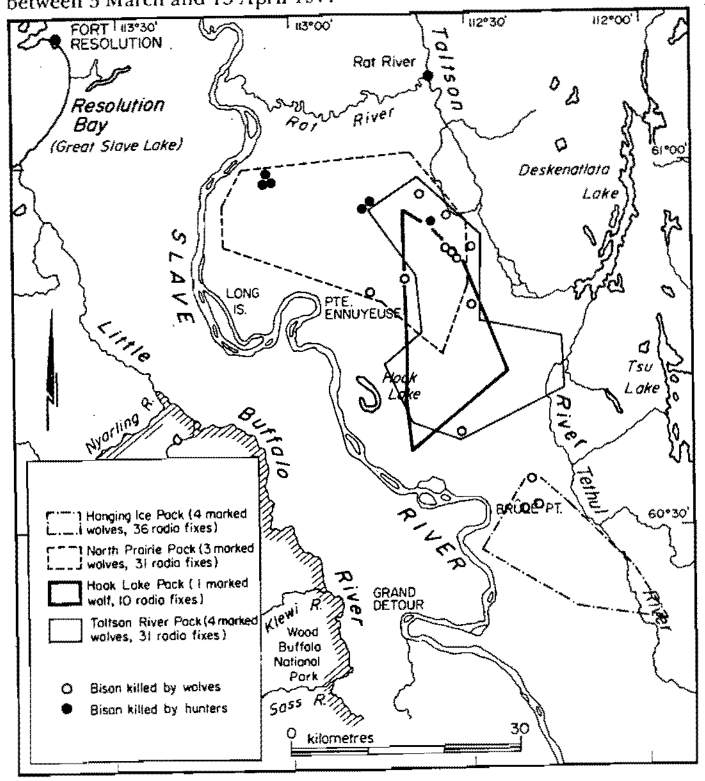


Table 1
Area of overlap between wolf pack home ranges during the period 3 March to 15 April 1977

Packs	Area of overlapping movements, km²
North Prairie and Hook Lake	60
North Prairie and Taltson River	153
Taltson River and Hook Lake	403

few days after contact with it had been lost. The collar had been chewed. Radio contact with the Hook Lake pack was maintained until the end of September 1977 and with the Hanging Ice pack until mid-December 1977.

Many of the transmitters failed prematurely because of faulty lithium batteries (AVM Co., pers. commun.). In some cases, problems with radio transmitters made it impossible to distinguish between emigrant wolves and radio failures.

4.2. Population estimates and territories

During winter 1976–77, 40–47 wolves were observed in the four packs east of the Slave River. Pack sizes were North Prairie pack, 12–14; Taltson River pack, 7–8; Hook Lake pack, 7–8; Hanging Ice pack, 14–17. The packs west of the Slave River were not radio-marked, and territories and pack sizes could only be estimated. If territories and total pack sizes of wolves on the west side of the river were similar to those on the east side of the river, then two packs, one containing 9 and the other containing 11 wolves, would have been expected west of the Slave River. One pack of at least 5 wolves was observed west of the Slave River in the Grand Detour area, and another pack of 8 wolves was also observed on the west side of the Slave River at a site approximately 3 km west of Hook Lake. Therefore, 53–60 wolves were observed in the SRL during 1976–77. Based on those observations and assumptions, an estimated six packs, containing from 58 to 69 wolves, were inhabiting the SRL bison ranges. The estimated wolf population on the SRL, corrected for lone wolves, for winter 1976–77 was 64–76.

Figure 4
Wolf pack home ranges determined by radio locations of marked pack members during the snow-free period, 15 April to 31 October 1977

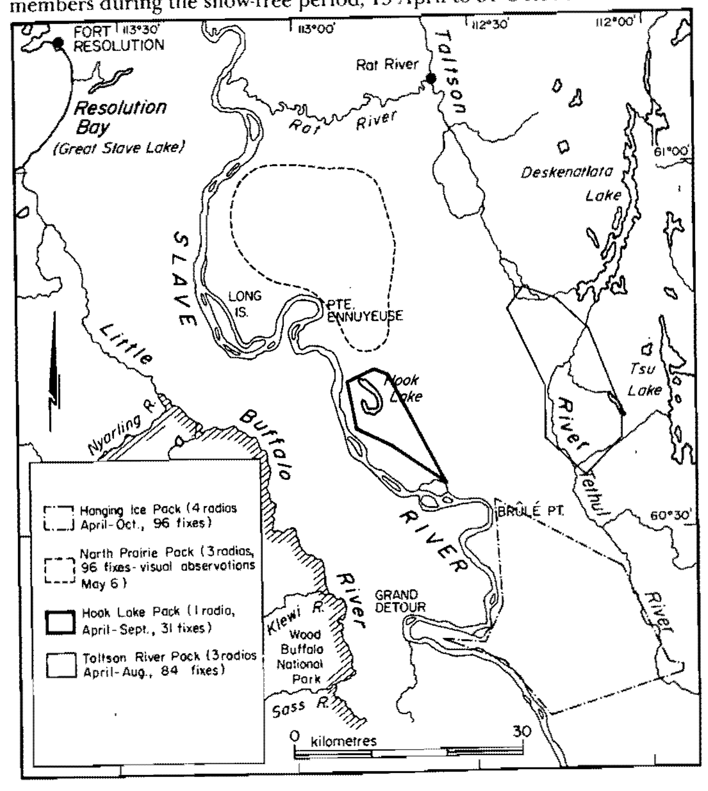


Table 2
Area of wolf pack home ranges from November 1976 to October 1977

Wolf pack	Min. area of movements during one year, km²	Min. area of movements during snow-free period, km²
North Prairie (November–April)	754	—
Hook Lake (March–October)	569	136
Taltson River (March–October)	973	233 (70*)
Hanging Ice (March–October)	655	563

* Represents movement of denning female.

During March and early April 1977, members of three packs were repeatedly radio-located in an overlap area (Fig. 3, Table 1). Wolves from separate packs overlapped spatially but not temporally and they used the same bison kills but never at the same time. One yearling male wolf from the North Prairie pack was killed and partially eaten at a site near a bison carcass that had been used by members of the Taltson River pack. The movements of the Hanging Ice pack did not overlap with any other radio-marked wolves throughout the year (Figs. 2 and 3).

With the onset of spring in mid-April 1977, the three northern packs split into small groups and moved into smaller, more clearly defined summer territories (Fig. 4). The Hanging Ice pack split into groups of one to five individuals but continued to move throughout most of the area they occupied during late winter (Fig. 4, Table 2). During spring and summer, movements centered on the whelping den. The dens of the Hook Lake, Taltson River, and Hanging Ice packs were located and, when examined, were found to have diggings that appeared to be many years old.

Table 3
Relative importance of major prey types in the diet of wolves from July 1975 to March 1978

Prey type	Est. wt. of prey type, kg	Frequency of prey type in scats‡ No.	Frequency of prey type in scats‡ %	Relative biomass of prey in diet sample§	No. of individuals eaten in diet sample*
Bison (*Bison bison*)	400.0*	166	22	77	3.5
Moose (*Alces alces*)	250.0†	32	4	10	0.7
Beaver (*Castor canadensis*)	12.5†	74	10	3	3.8
Hare (*Lepus americanus*)	1.2†	144	19	3	48.3
Muskrat (*Ondatra zibethicus*)	0.6	240	31	5	156.7
Duck (Anatidae)	0.5	112	14	2	88.0
Total¶		768	100	100	301

* Assumes an adult bison weighs 650 kg, a calf weighs 150 kg, and an equal number of calves and adults in diet. This is a conservative estimate of bison weights (refer to Table 49.1, Reynolds *et al.* 1982).
† Assumes an equal number of young and adults in sample (Floyd *et al.* 1978).
‡ Frequency of prey type identified in sample of 649 scats.
§ Calculated following methods of Floyd *et al.* (1978).
* Calculated by dividing weight in kilograms of prey type in sample by estimated weight of prey types.
¶ Totals for major prey types. Minor prey types were observed in 17% (158) of the scats. Minor prey types included: porcupine (*Erethizon dorsatum*), grouse (Tetraonidae), red squirrel (*Tamiasciurus hudsonicus*), wolf, various microtines, eggshells, unidentified feathers, and unidentified vegetation.

Radio contact with all four packs was lost by December 1977. Nine wolves were observed in the Hanging Ice territory in December 1977. Four or five wolves were observed in the Hook Lake territory and tracks of seven or eight wolves were observed in the Taltson River territory. These observations suggested a general decline of approximately 30%, which would have resulted in an early winter population estimate of 45–55 wolves. However, without radio-marked individuals in each pack, the accuracy of that estimate is uncertain.

4.3. Wolf dispersals

A mature, male, radio-collared wolf was observed on 17 May 1977 in the territory of the Hanging Ice pack. On 7 August 1977, it was killed by an automobile west of Cold Lake, Alberta, a linear distance in excess of 670 km (Van Camp and Gluckie 1979). Loss of radio contact from one adult male in the Hanging Ice territory and two adult females in the North Prairie area in May 1977 could have been the result of dispersals, but this could not be determined because of the high rate of radio failures. A yearling female that was radio-collared in March 1978 in the Raup Lake–Salt Plains area during a separate study in WBNP (S. Oosenbrug, pers. commun.) was observed following bison on 1 August 1978 with two other wolves in the North Prairie area, 160 km northeast of her capture location. Later in August, that wolf was observed within 2 km of the den found in the North Prairie area and, on several occasions, was radio-located in the area that had been occupied by the North Prairie pack during the previous year.

4.4. Food habits of wolves

Between July 1975 and March 1978, 649 wolf scats were collected from which 926 occurrences of prey items were identified. Six major prey types accounted for 83% (768) of the prey items (Table 3). Several minor types representing 17% (158) of prey item occurrences were also identified. To simplify analysis of the relative weight of prey types in the wolf diet, the minor prey types were not included in the sample.

In the analysis of major prey types, frequency of occurrence was 31% for muskrat (240 identifications of 768) and 22% for bison (166 identifications of 768). When frequency of occurrence was converted into relative biomass, bison constituted 77% of the weight of prey in the diet while muskrat represented only 5% by weight. Although muskrat remains occurred most frequently in the scat samples, they represented a relatively insignificant portion of the actual weight of prey consumed by wolves. Bison was the most important food item in the diet of wolves sampled. On a weight basis, bison was approximately seven times more abundant than moose in the diet of wolves in the SRL.

The diet of wolves varied from the season of snow cover to the snow-free season (Table 4). During the period of snow cover, bison and moose comprised 96% of the weight of major prey items in the diet sample, whereas muskrats, hares, and beavers collectively represented 4%. During the snow-free period, bison and moose represented 79% of the weight of major prey items in the diet sample, and muskrats, beavers, hares, and ducks collectively represented the remaining 21%. However, the frequency of occurrence of those items was much greater than that for bison or moose.

The diet also varied between wolf packs (Table 5). Bison comprised 85% of the weight of major prey biomass in the diet of the North Prairie pack and 73% of the major prey biomass in the diet of the Hook Lake pack during the snow-free period. However, bison represented only 11% of the major prey biomass consumed by the Taltson River pack during the snow-free period and were not found in the diet sample taken from the Hanging Ice pack at the same time. Beaver, hare, muskrat, and duck formed the bulk of the diets of the Hanging Ice and Taltson River packs but represented only about 22% and 9% of the diets of the Hook Lake and North Prairie packs, respectively, during the snow-free period.

The difference between predation and scavenging by wolves could only be determined in cases of direct observations of wolf attacks. However, during summer 1977, wolves in the vicinity of the Hook Lake den site were observed feeding on bison carcasses that had been abandoned by hunters. Several other instances of scavenging were also suspected. Therefore, diet analyses represented what wolves had been eating, not necessarily what they had killed.

4.5. Predation rates

From direct observations of radio-collared wolves at bison carcasses, the North Prairie pack killed and consumed one mature male bison, four mature females, and one calf between 8 November 1976 and 11 January 1977. Between 3 March and 15 April 1977, movements of the North Prairie, Taltson River, and Hook Lake packs overlapped continuously. Those three packs collectively killed and consumed six female bison, three calves, and one male and also visited four previous kills and at least six fresh hunter kills (Fig. 3).

During the same period, the Hanging Ice pack killed and consumed three female bison.

During 33 pack weeks (1 pack × 9 weeks + 4 packs × 6 weeks) of intensive radio tracking on the SRL in winter 1976–77, wolves killed and/or consumed 13 adult female bison, 2 adult males, and 4 calves. If that rate was consistent throughout the 22 weeks of winter, (8 November 1976 to 15 April 1977) the six wolf packs on the SRL could have killed and consumed 52 adult female bison, 8 adult bulls, and 16 calves in 132 pack weeks of effort during that winter.

4.6. Sex and age distribution of bison killed by wolves

Carcasses of 52 bison believed to have been killed by wolves were examined (Table 6). Adult female and subadult bison were killed by wolves in approximately the same proportion as they were found in the population. Calves were killed by wolves more frequently than they were found in the population and adult males were killed by wolves less frequently than they were found in the population (Van Camp and Calef, this publication). It was not possible to determine the disease status of most of the bison examined because the carcasses were nearly 100% consumed. Evidence of marrow depletion was not observed among the bison examined that were suspected of having been killed by wolves.

4.7. Hunting and other predation

From 1969 to 1974, an average of 179 bison per year were killed as a direct result of hunting (Table 7). That rate of harvest by hunting represents 8.9% of an estimated population of 2000 animals. From 1974 to 1976, when the SRL bison population was declining drastically, the absolute number of bison killed by hunters also declined, but the rate of kill continued to represent the same proportion of the total population, 8–10% per year. After resident and non-resident hunting seasons were terminated in 1977, GHL holders continued to kill bison at the rate of 4–8% of the population each year. Resident and non-resident hunters generally selected trophy bulls, whereas GHL hunters preferred subadults or small cows. There was little overlap in the sexes and ages of bison killed by wolves compared with those bison killed by hunters.

Observations of black bears (*Ursus americanus*) feeding on bison carcasses and following bison groups were made during the calving and post-calving seasons. However, no observations were made of black bears chasing, attacking, or killing bison.

4.8. Wolf control

The number of wolves observed during the bison total count surveys in March of each year reached a maximum of 45 in 1976 but declined to 25 in 1977 (Fig. 5). The control program during winter 1977–78 resulted in the removal of 34 wolves by trappers and 10 wolves by shooting from a helicopter. By the end of winter 1977–78, the SRL wolf population was reduced to a few pairs and small groups.

Table 4
Relative weight of major prey types in the diet of wolves during the period of snow cover from 8 November 1976 to 15 April 1977 and during the snow-free period from 16 April to 31 October 1977

	Frequency of prey type in scats*		Relative biomass of prey in diet sample†	
Prey type	Snow	No snow	Snow	No snow
Bison	54	66	88	70
Moose	8	15	8	9
Beaver	11	53	1	4
Hare	9	112	1	6
Muskrat	24	117	2	6
Duck	0	104	0	5
Totals	106	467	100	100

* Frequency of prey type identification in sample of 122 scats collected during the period of snow cover and 377 scats collected during the snow-free period.
† Calculated following methods of Floyd *et al.* (1978).

Table 5
Relative importance of six prey types in the diets of four wolf packs during the snow-free period from April to October 1977

	Frequency of prey type in scats*				% of prey weight in sample†			
Prey type	North Prairie	Taltson River	Hanging Ice	Hook Lake	North Prairie	Taltson River	Hanging Ice	Hook Lake
Bison	39	1	0	8	85	11	0	73
Moose	5	0	0	1	7	0	0	6
Beaver	24	16	2	6	4	13	3	4
Hare	22	33	41	4	2	17	36	2
Muskrat	19	69	29	33	2	33	25	14
Duck	6	51	42	4	1	26	36	2
Totals	115	170	114	56	101	100	100	101

* Frequency of prey identifications in total of 377 scats, 123 scats collected from North Prairie area April to October 1977, 125 scats from Taltson River den, 79 scats from Hanging Ice den, 50 scats from Hook Lake den.
† Calculated following methods of Floyd *et al.* (1978).

Table 6
Sex and age distribution of wolf-killed bison during 1976–77

	Male		Female				
	Subadult	Mature	Subadult	Mature	Calves	Sex-age undetermined	Total
Numbers of bison carcasses examined	1	5	1	23	16	6	52
Percent of sample	2	10	2	44	31	12	101

At least six wolves survived in the North Prairie area and three wolves survived in the home range area of the Hanging Ice pack. Only four wolves were observed during the March 1978 bison census survey. During winter 1978–79, 28 wolves were killed on the SRL as part of the control program and during the bison census survey in March 1979, only two wolves were observed (Fig. 5).

5. Discussion

5.1. Wolf territories, populations, and movements

Population estimates of wolves were based on the assumption that packs occupy stable territories. That concept has been supported by studies in Ontario (Kolenosky and Johnston 1967, Pimlott *et al.* 1969, Kolenosky 1972), Minnesota (Mech 1970, 1973, 1977; Peters and Mech 1975; Van Ballenberghe *et al.* 1975; Mech and Karns 1977, Harrington and Mech 1979), Isle Royale (Mech 1966, Jordan *et al.* 1967, Wolfe and Allen 1973, Peterson 1977), Manitoba (Carbyn 1980, 1981), and Alaska (Haber 1977, Stephenson 1978, Stephenson and Van Ballenberghe 1978, Gasaway *et al.* 1983). Most of those studies were conducted in areas where the ungulate prey base comprised moose, deer, elk, or a combination of those cervids. Cervids have efficient dispersal mechanisms and are relatively evenly distributed throughout their ranges. Only when the deer population became depleted did wolves in Minnesota leave their territories and trespass in the territories of neighbouring packs (Mech 1977). Trespasses were brief, short, usually ended in a return to the home territory, and often resulted in violent intraspecific confrontations. Carbyn (1981) recorded a trespass that was not food related in the high-density wolf population in Riding Mountain National Park.

Bison have a clumped distribution and concentrate in local areas during critical periods such as calving season and winter (Calef and Van Camp, this publication). Herd movements of greater than 20 km per day were observed in the SRL and are possible during any season. If the hunting strategy of wolves is to harass, wound, weaken, isolate, and finally kill mobile prey that travel in tight herds, then they must be able to follow that prey over long distances and for extended periods. When vulnerable prey are plentiful, perhaps wolves can afford to abandon wounded prey at a territorial boundary, but when prey are scarce, the advantages of following prey across territorial boundaries probably outweigh the disadvantages of risking conflict with wolves in a different territory.

Some of the data collected during this study do not fit the territorial concept. First, in an area where bison were concentrated during winter 1976–77, movements of 8 collared wolves overlapped to such a degree that it was impossible to separate them into packs until movements became more localized during the denning season (Fig. 3). Those 8 wolves attached themselves to at least three den sites on the SRL (Fig. 4). Second, a large number of radio signals disappeared at the end of winter. If the disappearance of territorial wolves was caused by radio failure, then 10 collared wolves should have been available for collection when 72 wolves were removed from that area during the winters of 1977–78 and 1978–79. No collared wolves were returned from collections between 1976 and 1979. Therefore, loss of radio signals was probably related to wolf dispersal. However, removal by chewing (Thiel and Fritts 1983) of collars containing failed radios is another possible explanation why no collared wolves appeared in the removal collections.

During summer 1978, a young female wolf radio-collared in WBNP during the previous winter was repeatedly located near the North Prairie den. It was possible that she could have been collared during a long-distance movement into WBNP and later returned to her original denning territory in the SRL from a winter hunting area. During the whelping season, collared wolves in the Hook Lake, Taltson River, and Hanging Ice packs used relatively small areas near their den sites, and overlapping movements were not observed (Fig. 4). If territorial boundaries remained consistent during the denning and whelping seasons but broke down with the onset of winter, then wolves could range widely, search for prey, and concentrate in areas where prey are abundant. If territorial imperatives are reasserted during the subsequent breeding and denning seasons, then those wolves with overlapping movements during the previous winter would disperse widely and set up new denning territories or return to home territories. Wolves apparently follow barren-ground caribou to and from winter ranges in a similar manner (Calef 1981). The abundance of wolves on the SRL during the late winter surveys of 1975–76 and 1976–77 and the large packs of wolves (including groups of 42, 33, and 30) that were observed on winter ranges in WBNP (Fau and Tempany 1976) could be explained in this manner. The dispersal of a large proportion of radio-collared wolves at the end of the winter, as observed in the SRL and in WBNP (S. Oosenbrug, pers. commun.), and the return of a radio-collared female to her home territory in the SRL during the whelping season could also be explained by that type of dispersal behaviour.

Wolf population estimates and trends based on the assumption of typical territorial behaviour could be misleading. If wolves from dispersed denning territories concentrated

Table 7
Bison kill statistics from the Northwest Territories as recorded from hunter licence returns for the calendar years 1968–79

	1968	1969	1970	1971	1972	1973	1974	1975	1976†	1977†	1978†	1979†
Government kill	10	50	5	60	15	10	11	—	0	0	0	0
General hunting licence	64	93	104	58	101	97	84	—	34	47	31	47
Resident	6	9	52	43	17	36	36	—	16	0	0	0
Non-resident	0	0	47	34	20	36	58	—	25	0	0	0
Totals	80	152	208	195	153	179	189	132*	75	47	31	47

Mean kill per year (1968–1976) 151 (Years of regulated bison hunting)
(1969–1974) 179 (Average of 6 years)
(1970–1974) 184 (Peak years of bison hunting)
(1977–1979) 42 (Unregulated GHL bison hunting after the decline)

* From Calef (1976).
† From 1976 to 1979, kill estimates included kills observed in the field that were not reported in licence returns.

on bison winter ranges and dispersed again during the breeding season, then the wolves using the bison ranges could be different from one winter to the next. Wolves may range more widely in winter, leaving their denning territories in search of prey. If wolves that were collared on the SRL bison ranges during winter 1976–77 congregated elsewhere during the following winter, then they would not have been in the wolf control area during the time of collection. That is another possible explanation for the reason why no radio-collared wolves appeared in the sample taken from the wolf control area during the winters of 1977–78 and 1978–79.

5.2. The impact of wolves on bison

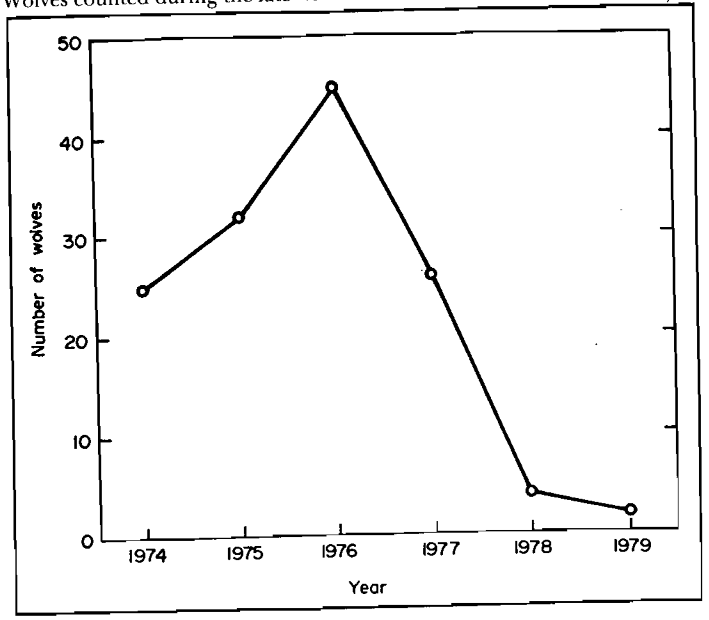
Bison were the most important prey of wolves in the SRL. However, the importance of bison is overrepresented in the total scat sample because a disproportionate number of scats were collected from the North Prairie area where bison were concentrated during the calving and post-calving seasons (Calef and Van Camp, this publication). When scats collected during the snow-free period were separated, analysed, and compared by home range, it was clear that bison were an important prey item only in the diets of the North Prairie and Hook Lake packs, whose dens were located in areas with greatest access to bison during the calving and post-calving seasons. Bison were relatively insignificant prey items for the Taltson River and Hanging Ice packs, whose dens were isolated from the areas of bison concentration during calving and post-calving seasons (Table 5). This observation supports the hypothesis that bison aggregations during the calving and post-calving seasons serve to reduce contact with denning wolves (Calef and Van Camp, this publication). The results of the food habits study suggested that wolves with greatest access to bison preyed most heavily on them and that denning wolves tended to remain near their dens rather than range widely to hunt for bison.

The difference between predation and scavenging by wolves is difficult to assess without direct observations of wolf attacks. In any case, bison that were wounded by hunters and bison carcasses abandoned in the field because of disease probably provided a large amount of food to wolves (Calef 1976). For example, during summer 1977, four bison cows, two of which were abandoned because of suspected tuberculosis, were killed by hunters within 2 km of the Hook Lake wolf den. Unmarked wolves, probably members of the Hook Lake pack, were observed feeding on those carcasses. Analysis of scats collected at the Hook Lake den indicated that the diet of wolves in the Hook Lake area was mainly bison.

Mech (1977) suggested that litter size and pup survival depended largely on the condition of the pregnant female at the end of winter, which is dependent on the amount of food available prior to and during the winter season. From March 1974 to March 1976, approximately 730 adult bison and 500 bison calves were lost to mortality factors other than human hunting (Van Camp 1978*a*). Independent of the direct cause of death, many bison carcasses were available for consumption by wolves. After 2 years with such an abundance of food, wolves wintering on the SRL could have produced large litters of healthy pups. A mean maximum finite rate of annual increase estimated for wolf populations in the wild is 1.36 (Keith 1983).

At the beginning of the telemetry study in fall 1976, the wolf population had just experienced a 2-year period of abundant food. During the same period, the bison prey base had been reduced by 52.6% (Van Camp and Calef, this publication, Fig. 1). It was speculated that an increasing wolf population was exerting heavy predation pressure on a declining bison population.

Figure 5
Wolves counted during the late winter bison censuses, March 1974–79



From March 1976 to March 1977, an estimated 191 adult and subadult bison were lost from the SRL population, calculated as follows: March 1976 total population estimate = 903 (Van Camp and Calef, this publication, Fig. 1), 1976–77 recruitment = 42 (Van Camp and Calef, this publication, Table 2), March 1977 total population estimate = 754 (Van Camp and Calef, this publication, Fig. 1); therefore, total adults and subadults lost = 903 + 42 − 754 = 191. Based on the estimated minimum rate of predation between 8 November 1976 and 15 April 1977 (22-week period of snow cover, see section 4.5), the total kill for the six wolf packs on the SRL was estimated to be 60 adult and subadult bison (52 females and 8 males). Thus, wolf predation during the winter accounted for a minimum 31.4% (60 of 191) of the adult and subadult bison lost during 1976–77.

Only 16 calf kills from wolf predation were estimated for the 22 weeks of winter during 1976–77 (8 November 1976 to 15 April 1977), based on direct observations of 4 kills (see section 4.5). That estimate of predation on calves may have been low because calf kills can be devoured within a day of the kill and surveys were flown only one to three times per week. Therefore, it is possible that additional calves were killed and consumed without being noticed. The total number of calves born in 1976 was approximately 190 (Van Camp 1977). Results from aerial surveys indicated that approximately 60 calves were lost at a constant rate during the period of snow cover. Therefore, observed wolf predation could account for at least 26.6% (16 of 60) of the calf mortality recorded during that 22-week period. Disease and starvation are possible factors that could have been responsible for additional losses of calves. Disease could also serve as a predisposing factor to bison mortality from wolf predation.

5.3. The impact of wolf control

The evidence obtained from radio-collared wolves and wolf food habit analyses supported the theory that wolf predation played a major role in the continued decline of the adult age class of bison and the poor recruitment of calves (mean = 3.9%) from 1973 to 1979 in the SRL.

As a result of wolf control, a substantial decrease in predation on bison occurred during winter 1977–78 compared with previous years. During calf surveys, the bison census, and intensive wolf surveys in winter 1977–78, only one adult bison kill and three calf kills were found. Four wolves were observed during the bison census in March 1978, compared with 25 in March 1977 and 45 in March 1976 (Fig. 5).

One pack of at least six wolves remained active in the denning territory of the North Prairie pack during summer 1978. Substantial losses of calves occurred in the North Prairie area during the post-calving season. However, wolf scats from other areas of the SRL not occupied by bison did not contain bison remains. Little evidence of wolf predation was observed during winter surveys in 1978–79, and only two wolves were observed during the March 1979 total coverage bison census. In spite of a record calf crop and continued wolf control, recruitment of calves did not improve following the winter of 1978–79, and a decline in the bison population was again recorded (Jalkotzy 1979). Therefore, during that winter wolves were not directly responsible for the bison decline. An anthrax outbreak during summer 1978 (Stephenson 1979) complicated the trend analysis after that season. Other mortality factors, such as disease, hunting pressure, and winter severity, combined with wolf predation, collectively exerted continuous heavy pressure on bison survival. Difficulty in finding bison carcasses increased the problem of determining causes of the continued decline in the population.

5.4. The impact of hunters and other potential predators on bison

Between 1969 and 1972, the SRL bison population was estimated to be about 2000 and recruitment was estimated to be approximately 10% per year. Harvest by hunters averaged approximately 8.8% per year. During 1974–76 recruitment of bison to the population dropped to an average of only 3.0% per year (Van Camp and Calef, this publication), but hunters killed approximately 9.6% of the bison population annually. Wolf predation undoubtedly accounted for additional losses during that period and factors such as disease and severity of winter could also have contributed.

The hunter kill statistics (Table 7) reflect minimum estimates because of uncounted wounding losses and unreported kills. The reporting of bison kills to the government was not a legal requirement for GHL hunters and was not always complete. For example, during fall 1976, a licensed outfitter killed at least 33 bison but reported only 25. During winter 1976–77, field workers observed 25 kills made by hunters from the Fort Resolution area, but only 15 of them were reported to the area game office. During summer 1977, another group of hunters killed 6 bison but reported only 2. Based on those examples in 1976–77, the reported kill represented only about 65.6% (42 of 64) of the observed kill. Whole carcasses were often abandoned by hunters because of suspected disease and were not reported in licence returns. Actual kills could have been considerably higher from 1968–75 than the numbers reported to game offices. Kill estimates reported in Table 7 for 1976–79 include kills observed in the field that were not reported in licence returns. Those should still be regarded as minimum estimates.

During 1976–77 hunters reported killing 75 bison, of which nearly all were adults and subadults; thus, hunting pressure accounted for a minimum of 39.3% (75 of 191) of the adults and subadults lost during that year. Winter wolf predation and hunting pressure combined accounted for 135 (70.7%) of the 191 adults and subadults lost during 1976–77. Many of the remaining losses could be attributed to unobserved kills (both wolf and hunter) during winter and to wolf predation during the snow-free period. Disease is another potential source of mortality of SRL bison (Broughton, this publication) and it may also serve to increase vulnerability of animals to wolf predation; however, the number of losses resulting directly from disease could not be determined.

Apart from wolves and humans, another possible predator of bison in the SRL is the black bear. In Idaho, black bears caused significant mortality in elk calves (Shlegel 1976, Leege *et al.* 1978). Black bears are abundant in summer throughout most of the SRL and may have killed bison calves during that season.

Seasons for resident and non-resident hunting of bison were closed in fall 1977. The GHL holders voluntarily agreed to reduce their harvest to 25 bison; however, they harvested a mean of 42 bison per year from 1977 to 1979 (Table 7). During the early 1970s, GHL hunters harvested approximately 5% of the herd per year. As the population became smaller, the total number of bison killed by GHL hunters decreased but the proportion of the herd harvested remained approximately the same (4–8%) from 1977 to 1979. From 1973 to 1979, recruitment to the SRL bison population averaged only 3.9% per year. The kill by GHL hunters alone was thus greater than the annual recruitment to the population during the entire period. Population decline was inevitable as long as rates of harvest exceeded recruitment. Residual predation following the wolf control program contributed further to the population decline. Censuses between 1980 and 1983 showed continued decline in the SRL bison population (Van Camp and Calef, this publication).

Diseases affecting bison

Eric Broughton

1. Abstract

Bison in the Slave River lowlands (SRL) and Wood Buffalo National Park (WBNP) have shown high rates of disease infection, primarily with tuberculosis, brucellosis, and anthrax. Examinations and/or testing for tuberculosis and brucellosis in bison were conducted in WBNP between 1950 and 1974 and in the SRL between 1964 and 1974. Tuberculosis infection rates averaged 40% in WBNP (range 15–56%) and varied from 25 to 40% in the SRL. Field examination of bison shot by recreational hunters in 1974 in the SRL revealed a high level of tuberculosis-like lesions. Brucellosis infection rates averaged 30% in WBNP (range 6–62%) and 38% in the SRL. The first outbreak of anthrax killed 281 bison at Hook Lake, Northwest Territories, in July 1962. Attempts to control the disease included depopulation and vaccination. Anthrax and associated control measures have resulted in the death of approximately 1600 bison in the SRL and WBNP since 1962.

2. Introduction

The Government of Canada moved 6673 plains bison (*Bison bison bison*) from Wainwright, Alberta, to Wood Buffalo National Park (WBNP) during 1925–28 (Soper 1941). Plains bison in Buffalo National Park, Wainwright, were not tested for tuberculosis (*Mycobacterium bovis*) prior to shipment to WBNP as was originally planned (Lothian 1981). The four annual shipments consisted of young animals in age classes of 1, 2, and 3-year-olds with females being in the majority. In WBNP, resident wood bison (*Bison bison athabascae*) and the introduced plains bison interbred and formed a hybrid population that increased rapidly. A bison management program, established in WBNP in 1952, involved periodic slaughter of animals and marketing of bison meat commercially. That program provided an excellent opportunity to collect biological data and information on the health of the bison population.

The first known outbreak of anthrax (*Bacillus anthracis*) in the Slave River lowlands (SRL) occurred during July 1962 in the vicinity of Hook Lake, Northwest Territories (NWT), whereas that in WBNP occurred near Hay Camp Station and the Lake One area during summer 1964. Corrals were constructed, in WBNP at Lake One and in the SRL at Hook Lake in 1964, for the purpose of vaccinating bison against anthrax. The corrals that had been used in the commercial meat operation at Sweetgrass and Hay Camp in WBNP were also used in the vaccination program. Numerous outbreaks of anthrax since 1962 and subsequent control measures have resulted in an assessment of the effect of that disease on northern bison. Commercial bison harvests and vaccination programs provided an opportunity to examine the bison populations in the SRL and WBNP for diseases such as tuberculosis, anthrax, and brucellosis (*Brucella abortus*). This paper reports and discusses the results of those examinations.

3. Methods

Tuberculosis was the first disease investigated in northern bison populations. Between 1950 and 1967, bison killed during annual slaughters as part of the management program and as a by-product of a commercial meat production program in WBNP were examined postmortem for tuberculosis by veterinary personnel of the Canada Department of Agriculture, Health of Animals Branch (H of A), (Novakowski 1957*b*, 1958; Choquette *et al.* 1961; Fuller 1962; Choquette and Broughton 1967*a*). Tuberculin testing of live bison using bovine tuberculin was also carried out in WBNP from 1957 to 1959 (Novakowski 1957*b*, 1958; Choquette *et al.* 1961). In addition, testing and/or examination took place in the Salt Plains, Lake Claire, Sweetgrass, and Hay Camp areas. Bison slaughtered in the Grand Detour area of the SRL in 1964 and 1965 were subjected to postmortem examination for tuberculosis (Novakowski 1965). Some of the bison shot by recreational hunters in the SRL in 1974 were examined in the field for evidence of tuberculosis (Coupland 1975).

The incidence of brucellosis in bison in WBNP was determined between 1956 and 1974. Blood was collected from the heart during abattoir processing of slaughtered bison or from the jugular vein at field kills. In 1957 and 1958, blood samples were tested using the *Brucella* rapid plate test technique (Novakowski 1957*b*, 1958). In 1956, and between 1959 and 1974, blood samples were tested for brucellosis using the standard tube serum agglutination test (Choquette *et al.* 1978). The interpretation of bison test results was based on the criteria established by H of A for bovine brucellosis testing programs. In 1970 and 1974, 27 and 272 bison blood samples, respectively, were collected in conjunction with the anthrax program at Hook Lake and tested for brucellosis. At roundups, blood was collected from the tail vein. Several bison shot by recreational hunters in 1974 were also tested (Coupland 1975). Blood serum samples were analysed by H of A using the standard tube agglutination test.

Anthrax investigations began in 1962 following the initial outbreak in the Hook Lake vicinity of the SRL. Periodic aerial surveys were conducted between 1962 and 1971 during mid- to late summer of each year to determine the number of bison deaths caused by anthrax in the SRL and WBNP. Aerial surveys, during years in which there were outbreaks, were supplemented by ground searches for carcasses. Carcasses were promptly disposed of by liming and burial under mounds of earth (1962–64) and, after 1967, by incineration using fuel oil and wood and then burial of the remains in the incineration pit. In late November 1964 and in early March 1965, bison in the Grand Detour area on the west side of the Slave River were slaughtered in a depopulation program to control the spread of anthrax following recommendations made by the Anthrax Committee (Novakowski 1965). Anthrax vaccinations of bison in WBNP were conducted in 1965 and 1966 and from 1968 to 1971. Vaccinations were also conducted at Hook Lake in 1965 and 1966 and annually from 1972 to 1975 inclusive.

Table 1
Incidence of tuberculosis in bison tested and examined postmortem in Wood Buffalo National Park, 1950–67

		Postmortem examination		Tuberculin testing		
Year	Location	No. examined	No. positive (%)	No. examined	No. positive (%)	Reference
1950	Salt Plains	79	23 (29)	—	—	Fuller 1962
1952	Lake Claire area	218	44 (20)	—	—	Fuller 1962
1952	Hay Camp	245	113 (46)	—	—	Fuller 1962
1952–56	Hay Camp	1508	609 (40)	—	—	Fuller 1962
1957	Sweetgrass	418	131 (31.3)	1065	154 (14.5)	Novakowski 1957*b*
1958	Sweetgrass	273*	?	469	90 (19.1)	Novakowski 1958
1959	Lake Claire area	436†	219 (50.2)	1116	151 (13.5)	Choquette *et al.* 1961
1963	Hay Camp	155	62 (40.3)	—	—	Novakowski and Choquette 1963
1966	Hay Camp	162	50 (30.9)	—	—	Choquette and Broughton 1967*a*
1967	Hay Camp‡	337	131 (38.9)	—	—	Choquette and Broughton 1967*a*
	Total	3403	1320 (38.8)	2650	395 (14.9)	

* Not included in the total.
† 357 of these bison were also tested, and are included in the 1116 bison shown as tested.
‡ Bison were corralled at Sweetgrass but were moved to Hay Camp where they were slaughtered and examined.

Table 2
Number, age, sex, and incidence of tuberculosis in bison slaughtered at Grand Detour in November 1964 and March 1965

		No. examined		Incidence of TB: no. positive (%)		
Year	Age class	Male	Female	Male	Female	Total number positive (%)
1964*	Calf	7	3	0 (0)	0 (0)	0 (0)
	1	1	9	0 (0)	0 (0)	0 (0)
	2	6	11	2 (33)	5 (46)	7 (41)
	3	8	28	3 (38)	13 (46)	16 (44)
	4+	2	13	2 (100)	7 (54)	9 (60)
	Total	24	64	7 (29)	25 (39)	32 (36)
1965†	Calf	6	8	0 (0)	2 (25)	2 (14)
	1	5	1	0 (0)	0 (0)	0 (0)
	2	19	33	6 (32)	4 (12)	10 (19)
	3	17	83	6 (35)	20 (24)	26 (26)
	4+	7	13	2 (29)	3 (23)	5 (25)
	Total	54	138	14 (26)	29 (21)	43 (22)

* Only 88 of 189 animals slaughtered were examined.
† Only 192 of 333 animals slaughtered were examined.

4. Results

The rate of tuberculosis infection in bison in WBNP between 1950 and 1967, based on postmortem examination, ranged from 20 to 50% and averaged 38.8% (Table 1). During the 1959 study, 357 of the 1116 bison that underwent tuberculin testing were examined postmortem. There were 58 non-reactors showing tuberculous lesions and 19 reactors that did not exhibit visible lesions. Experience in the field has shown that a few animals, although infected, do not give a good response to tuberculin testing. That situation includes animals that are in an advanced stage of the disease and animals in which infection is localized in one or two lymph nodes and has become inactive. Also, it is not uncommon for an animal that has reacted to a tuberculin test and has been slaughtered not to exhibit any visible gross lesions of tuberculosis during postmortem examination. In 1964, as a result of the depopulation program slaughter at Grand Detour in the SRL, 88 bison carcasses were examined for tuberculosis, and 32 animals were infected (36%); in 1965, 192 carcasses were examined and 43 animals (22%) were infected (Table 2). The incidence of tuberculosis in those bison slaughtered at Grand Detour in 1964 and in 1965 averaged 26.8%. A higher infection rate in females than in males was evident in November 1964; however, the reverse was true in March 1965. There was a significantly higher rate of infection in females 2 years of age and older in the November sample (39%) than in the March collection (21%) (Table 2). A high percentage (43%) of 25 bison shot by recreational hunters in the SRL and examined in the field in 1974 exhibited lesions suggestive of tuberculosis (Coupland 1975).

Testing of bison blood samples from WBNP in 1957 and 1958 yielded brucellosis reactor rates of 39% (N = 200) and 49.8% (N = 640), respectively (Choquette *et al.* 1978). In

Table 3
Brucellosis test results in Wood Buffalo National Park, 1959–74

Year	Number tested	Suspicious	Positive	% positive
1959	311	32	116	37.3
1960	76	9	38	50.0
1961	378	22	161	42.6
1962	63	9	13	20.6
1963	143	6	19	13.3
1964	193	10	34	17.6
1965	131	11	8	6.1
1966	161	13	27	16.8
1967	333	19	74	22.2
1971	164	2	65	39.6
1974	113	8	70	62.0
Total	2066	141	625	30.2

1956, a small sample (11) from Hay Camp showed a 27% positive rate for brucellosis (Fuller 1962). On an average, 30% of the blood samples collected at the time of slaughter in WBNP from 1959 to 1974 were positive for brucellosis (Table 3). The reactor rates during this 15-year span varied from a low of 6% in 1965 to a high of 62% in 1974 (Choquette *et al.* 1978). The incidence of brucellosis in bison sampled at Hook Lake in 1970 and 1974 was 26 and 39%, respectively, for a 2-year average of 38.1% (Table 4). Of 11 blood samples taken from hunter-killed bison in 1974, six (54.5%) tested positive for brucellosis (Coupland 1975).

The first anthrax outbreak in the SRL in 1962 killed 281 bison (Table 5) and was confined to the east side of the Slave River around Hook Lake (Novakowski *et al.* 1963). The disease killed an additional 281 bison in 1963, with the major die-off occurring on the west side of the Slave River in the Grand Detour area (Cousineau and McClenaghan 1965). In 1964, the disease killed 202 bison at Grand Detour, 44 bison at Hook Lake, and 53 bison in WBNP, where it was first confirmed in the park (Choquette *et al.* 1972). No further outbreaks of anthrax were reported in bison in the SRL until 1971, when 37 animals in the Hook Lake area died from the disease (Table 5). However in WBNP, an outbreak of anthrax in 1967 resulted in the death of 120 bison (Choquette and Broughton, 1967*b*). In 1968 only one death attributable to anthrax was recorded in WBNP. The last anthrax outbreak was recorded in 1978, when 39 bison died in the SRL and approximately 40 died in the Salt Plains area of WBNP (L. Colosimo, pers. commun.; Table 5). A total of at least 1098 bison in those northern herds died from 1962 to 1978 as a direct result of this disease. In addition, 189 bison were killed in November 1964 and 333 were killed in March 1965, for a total of 522, as a result of the depopulation program in the Grand Detour area to prevent the spread of anthrax (Novakowski 1965).

In WBNP, 3591 and 3587 bison were vaccinated against anthrax in 1965 and 1966, respectively (Choquette *et al.* 1972). In 1968, 1969, 1970, and 1971, respectively, 940, 3021, 3452, and 779 bison were vaccinated (Choquette *et al.* 1972). Seven hundred bison were vaccinated against anthrax at Hook Lake in 1965 and 557 in 1966 (Choquette and Broughton 1967*a*). An additional 1131 Hook Lake bison were vaccinated from 1972 to 1975.

Table 5
Number of bison deaths attributable to anthrax in the Northwest Territories and Alberta, 1962–78

	Northwest Territories		Alberta	
	East of Slave River	West of Slave River	Wood Buffalo National Park	
Year*	Hook Lake	Grand Detour	Hay Camp Area	Lake One Area
1962	281	—	—	—
1963	12	269	—	—
1964	44	202	46	7
1967	—	—	—	120
1968	—	—	—	1
1971	37	—	—	—
1978	12	27	40	—
Total	386	498	86	128
Grand total				1098

* No deaths attributable to anthrax were recorded for 1965, 1966, 1969, 1970, or 1972 to 1977 inclusive.

5. Discussion

5.1. Effects of diseases on northern bison

Bison in WBNP and the SRL have shown high incidences of infections with tuberculosis and brucellosis. Such high rates of infection can be considered seriously detrimental to the health of northern bison and have probably limited their survival and productivity. However, it has not been possible to quantify the rate at which tuberculosis and brucellosis have limited those herds. In addition to causing direct mortality, diseases can weaken the general health of animals without causing death and thereby predispose them to predation. Furthermore, several outbreaks of anthrax since 1962 have resulted in substantial losses of bison from those herds.

A male bison shot near Fort Smith, NWT, in 1946 was confirmed tubercular (Wm. Fuller, pers. commun.). Tuberculosis-like lesions were first observed in bison in WBNP in 1947–48 (Choquette *et al.* 1961). Bison in the SRL emigrated from WBNP (Van Camp and Calef, this publication) and probably brought the disease with them. Recreational hunters in the SRL reported a high incidence of tuberculosis-like lesions in bison between 1968 and 1976. Incidence of tuberculosis in bison at Hook Lake in 1974 was similar to that in WBNP. The economic importance of tuberculosis is difficult to assess, but it is estimated that in cattle infected animals lose 10–25% of their productive capacity in terms of feed efficiency, weight gain, and milk production (Blood *et al.* 1983). In view of the incidence of tuberculosis in bison of the SRL, the disease probably causes at least a 15% loss of productive capacity. Tuberculous orchitis and metritis were reported in bison in WBNP (Choquette *et al.* 1961). Novakowski's (1965) data suggested that the rate of tuberculosis infection in bison increased with age of the animals. Although there were significant differences between sexes and within sexes between years in the incidence of tuberculosis in bison slaughtered at Grand Detour in 1964 and 1965 (Table 2), the reasons for those differences are not known. Interpretation of the data was confounded by biased samples because of the meat salvage operation and exclusion of older males from the test sample (Novakowski 1965). Therefore, the actual rate of infection in those herds could not be determined.

Table 4
Brucellosis test results, Hook Lake, 1970 and 1974

Year	Sex of animal	No. tested	Suspicious	Positive	Reaction rates % positive
1970	unknown	27	1	7	25.9
1974	unknown	4	—	1	25.0
1974	female	209	10	83	39.7
1974	male	59	5	23	38.9
Total		299	16	114	38.1

Brucellosis has been a serious disease in northern bison since at least 1956, when it was first reported in WBNP. Brucellosis causes reproductive loss in cattle by causing frequent returns to oestrus, temporary or permanent sterility, weak calves, loss of calf production through abortion, and loss of some animals as a result of acute metritis associated with retained placentas (Meagher 1973; Choquette *et al.* 1978). It probably causes similar effects in the bison of the SRL and WBNP and may have significantly reduced their reproductive capacity. The localization of brucellae in the testicles causes orchitis, which results in little or no sperm production in advanced cases (Choquette *et al.* 1978). Dominant males tend to be in the older age classes; therefore, brucellosis could have an additional negative effect on reproductive success in the population by causing sterility in the dominant males.

Abortion was observed in bison at Sweetgrass in WBNP (K. Cooper, pers. commun.). Orchitis, associated with brucellosis, was observed frequently in adult males during slaughters in WBNP. In cattle, brucellosis usually causes abortion in infected animals at the first pregnancy and occasionally during the second pregnancy. After that, infected animals usually give birth to a full term fetus and will seldom abort again unless an "abortion storm" occurs, when almost all pregnant females will abort. The frequency of abortion storms is related to the degree of continual exposure to the *Brucella* organism in the environment.

Fuller (1962) compared conception rates of bison from Elk Island National Park (EINP), the National Bison Range (NBR), Montana, Yellowstone National Park (YNP), and WBNP. Conception rates in EINP and the NBR were 85 and 86%, respectively. The rates in WBNP and YNP were both 65%. Brucellosis is present in bison in WBNP and YNP but not in EINP or the NBR. The expected calf crop in WBNP is about 35–40% of the herd whereas the observed calf crop is 20–25% (Fuller 1961). Brucellosis-induced abortion in late pregnancy may contribute to this difference between observed and expected calf percentages. Novakowski (1965) reported pregnancy rates of adult bison cows in the Grand Detour area in November 1964 and March 1965 of 38 and 15%, respectively. One could speculate that a reduction in birth rate rather than an increase in calf mortality accounts for the lower calf percentages observed in that northern bison herd, although there are no data to substantiate that. Measurements of fetuses obtained at a slaughter in YNP demonstrated a great variation in size, indicating a prolonged rut (Rush 1932). That extended rut may have been an effect of brucellosis resulting in frequent returns of oestrus. Similarly, the size of fetuses that were examined during bison slaughters in WBNP varied (Wm. Fuller, pers. commun.). Also, during annual roundups and slaughters in WBNP, late-born calves, evident by orange body colour, were observed regularly, which indicated returns to oestrus, repeated breeding, and an extended rut.

The source of the anthrax organisms that caused the initial outbreak at Hook Lake in 1962 is unknown. The organism may have been present in the Hook Lake area prior to the documented outbreak in 1962, but that is now impossible to confirm. Also, it has been suggested that the disease was introduced into the area from Alberta by outfitter-owned horses. However, when tissues from the carcasses of 16 horses that died at Hook Lake in winter 1960–61 were sent to the Alberta veterinary laboratory, no specific diagnosis was made. No cases of anthrax had been reported in the area of Alberta where the horses originated.

Anthrax organisms were most probably brought by migratory birds to the Hook Lake area from endemic anthrax areas in the United States, such as Louisiana and Texas. Waterfowl and other migratory birds can transport anthrax spores in their intestinal tract from endemic areas and establish foci of anthrax-spore contamination at stopover or nesting areas. Anthrax occurred at Lake One, WBNP, in July 1967 and was present in the Fort Vermilion area of Alberta in 1967. Investigation of the outbreak near Fort Vermilion revealed that the first losses had occurred in May near a small water body that had been used by a large number of migratory waterfowl. Viable anthrax spores were recovered from the cloaca of gulls that had been feeding on anthrax-infected bison carcasses at Hook Lake in 1964 (G. Cousineau, pers. commun.).

Anthrax has had a considerable negative impact on the bison of the SRL and WBNP through direct losses. Indirect effects on productivity are not known. Anthrax and attempted control measures by depopulation resulted in the death of approximately 1600 bison on the SRL and in WBNP since 1962. Deaths associated with herding and handling of bison during anthrax vaccination programs were not determined and are not included. Bison males appeared to be more susceptible to anthrax infection than females, based on the fact that more male carcasses were found during outbreaks. The bison rut normally occurs from mid-August to early September and coincides with the latter part of the usual period for anthrax outbreaks, between late June and early September. The loss of adult males during the rut could have a marked effect on herd productivity. Disturbing the animals by searching for and destroying infected carcasses prior to and during the rut could also adversely affect reproductive performance.

5.2. Disease control

It is possible to eradicate brucellosis and tuberculosis by rigorous testing and slaughter of reactors. Both *B. abortus* and *M. bovis* are relatively susceptible to direct sunlight and are rapidly destroyed. In moist, protected environments both organisms can survive for long periods; however, the primary source for continued spread of the two diseases is the infected animal, not the contaminated environment (Blood *et al.* 1983). Cattle infected with *M. bovis* excrete the organism in exhaled air and in feces and urine. A cow infected with *B. abortus* sheds the organism at parturition in the placental membranes and fluids and in the fetus. In males, the genital organs are usually infected. Semen contains large numbers of *Brucella* during the early acute stage of infection and may result in the infection of bred females. The known high incidence of brucellosis and the suspected high level of tuberculosis suggest that the implementation of an eradication program would likely result in the elimination of the SRL and WBNP bison populations.

Anthrax is undoubtedly the most difficult to eliminate of the three major diseases infecting northern bison. The sporulation by *B. anthracis* renders the task of eliminating the organism from the SRL and WBNP virtually impossible. Anthrax spores have remained viable for over 60 years under certain laboratory conditions (Sterne 1959). It is unlikely that the spores could survive for an indefinite period of time in a natural environment. However, periodic outbreaks will result in the continued contamination of an area, a recurring situation in the SRL that creates additional sites of contamination to further disseminate the disease.

Vegetation, bison diets, and snow cover

Hal W. Reynolds
Donald G. Peden

1. Abstract

Studies of herbage production and plant species composition were conducted in the Hook Lake area of the Slave River lowlands (SRL) during 1974 and 1975. The mean annual herbage yield for wet meadows in 1974 and 1975 (4480 kg/ha and 4320 kg/ha, respectively) significantly exceeded that for dry meadows (2680 kg/ha and 1880 kg/ha, respectively). The most common range plants were slough sedge (*Carex atherodes*) and reed grasses (*Calamagrostis* spp.) which comprised, respectively, 49 and 18% of the composition of wet meadows and 1 and 64% of dry meadows.

Diets of free-ranging bison (*Bison bison*) were determined by histological examination of fecal samples. Seasonal bison diets contained 29 different plant species of which 12 contributed greater than 1% in at least one season. Slough sedge and reed grasses were the most common foods for bison in all seasons ranging, respectively, from 42 and 35% of the diet in winter to 77 and 15% in spring. Bison showed a preference for feeding on wet meadow vegetation. Herbage yield was not limiting to the production of bison in the SRL.

Snow hardness, depth, and density were measured in areas where bison did and did not feed during winter 1974–75. Mean hardness of snow was 250% greater ($P < 0.01$) on sites where bison did not feed than on feeding sites. Mean snow depths and densities differed more between time periods than between feeding sites and sites where bison did not feed. Snow hardness appeared to be the principal characteristic of snow cover influencing bison use of feeding sites.

2. Introduction

The Slave River lowlands (SRL) have been important rangelands for wild bison (*Bison bison*) since at least the early 1940s. Although the herd of hybrid bison occupying the SRL exceeded 2000 animals in the early 1970s, it now numbers less than 400. This study was conducted in the Hook Lake area of the SRL to determine herbage production and plant species composition of the range, seasonal food habits of bison, plus snow hardness, depth, and density in areas used by bison for feeding sites and in sites that were not used for feeding.

Bison diet information has been published by Meagher (1973), Peden *et al.* (1974), Peden (1976), Reynolds (1976), Reynolds *et al.* (1978, 1982), Van Vuren (1982), Campbell and Hinkes (1983), Van Vuren and Bray (1983), and Van Vuren (1984).

Snow cover can affect movements, feeding behaviour, and abundance of northern ungulates, and the depth of snow can restrict winter range use (Formozov 1946, Nasimovich 1955, Edwards 1956, Telfer 1967, Kelsall 1969). Some researchers have described the effects of snow hardness and density on wintering ungulates (Lent and Knutson 1971, Kelsall and Prescott 1971, Coady 1974, Van Camp 1975). When compared with three other species of North American ungulates (moose [*Alces alces*], wapiti [*Cervus elaphus*], and white-tailed deer [*Odocoileus virginianus*]), bison exerted the greatest weight load on track and possessed relatively short legs, indicating that they would experience greater difficulty in moving through deep snow (Kelsall and Telfer 1971, Telfer and Kelsall 1979). The SRL bison herd occupies the northeastern fringe of present day bison range in North America where snow cover exists for about 7 months of the year. Therefore, snow can be expected to be a major determinant in range use and behaviour of that population. Adaptation to snow is a key factor regulating distribution of northern mammals (Formozov 1946, Telfer and Kelsall 1979, 1984).

3. Methods

3.1. Range production and composition

Herbage yield and plant species composition estimates were determined using sample plots of 0.25 m² from randomly located sample transects (Fig. 1) in each of two vegetation types, wet meadows and dry meadows, in November 1974 and August 1975 and utilizing methods described by Reynolds *et al.* (1978). Mean annual herbage yield (kg/ha) was estimated for the two meadow types and also for individual plant species in each meadow type based on the data from the clipped plots and the area of each meadow type. Plant species composition by percentage was calculated for each meadow type.

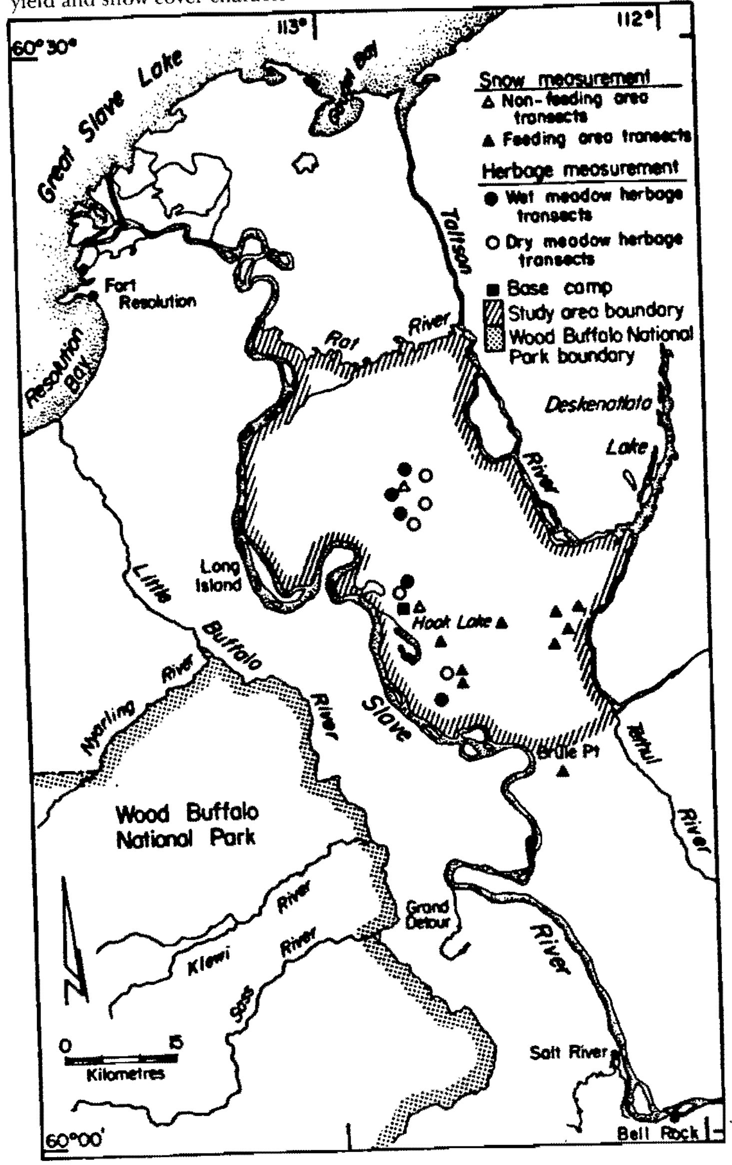
3.2. Food habits

Fecal samples were collected approximately twice monthly at bison feeding sites on meadow range in the Hook Lake study area from July 1974 through August 1975 according to methods described by Reynolds (1976) and Reynolds *et al.* (1978). A microhistological technique was used to determine the frequency of occurrence of each plant species identified in each of eight diet samples that were pooled to represent four seasonal diets of bison (Reynolds *et al.* 1978).

3.3. Snow cover characteristics

In winter 1974–75, snow depth, density, and hardness were measured during November–December, February,

Figure 1
Transect sites in the Hook Lake study area for measurements of herbage yield and snow cover characteristics



March, and April at bison feeding sites and at sites where bison had not grazed (Fig. 1). Measurements of the undisturbed snow at the edge of individual bison feeding craters were taken within feeding areas as soon as possible after bison had been observed feeding at the site, in most cases within 24 h. To represent areas where bison did not feed, snow measurements were systematically taken along two 1-km transects (Fig. 1). Transects were selected in open meadow habitat containing known bison food plants to test the hypothesis that bison do not feed in large open meadow areas during winter because snow conditions are more severe than in sheltered habitat. One transect was located in the northern part of the study area in a large, open meadow and the second was located centrally, in a large meadow containing scattered patches of aspen (*Populus tremuloides*) and willows (*Salix* spp.).

Snow hardness was measured with a Rammsonde penetrometer (Lent and Knutson 1971). A modified conical point with sides at an angle of 120° to the shaft was used in soft snow in place of the standard 60° point to increase sensitivity of the penetrometer. Values obtained with the modified point were converted to standard hardness values using the formula: $R = 0.27\ (R_m^{0.82})$, where R = corrected ram hardness and R_m = hardness number obtained with the modified cone (Geotest Instrument Corporation 1970). Ram hardness number, R, is an index representing the resistance, in kilograms of force, to the penetration that a snow layer offers to the cone of the penetrometer and is regarded simply as a resisting force (Benson 1962). When each depth increment is multiplied by its ram hardness number and those values are summed from the surface to the total depth of the snow layer, an integrated ram hardness number is obtained. Because the ram hardness number is expressed in kilograms of force, the integrated Rammsonde value is in kilograms of force per centimetre of snow thickness (kg-f/cm) where 1 kg-f/cm = 0.098 joule. The integrated ram hardness value indicates the total amount of work required to overcome the resistance as the penetrometer moves through a given thickness of snow (Benson 1962).

Snow depth was measured with a metre stick. Snow density was measured with an Adirondack snow sampler, which consisted of a calibrated fibreglass tube with a cutting edge at one end. The tube was pushed through the snow vertically to the ground. Snow depth on the outside of the tube was recorded and then the tube was withdrawn maintaining an intact snow column inside. The tube plus the snow column inside were weighed on a scale calibrated in equivalent centimetres of water. Density was calculated by dividing centimetres of water by centimetres of snow and was expressed in grams per cubic centimetre.

Analyses of variance were used to test for differences in hardness, depth, and density measurements between feeding areas and areas where no feeding occurred and among sample periods. Tukey's multiple comparison test (Snedecor and Cochran 1967) was used to determine specific mean differences among sample periods. Correlation coefficients between snow hardness and snow density values were computed for feeding areas and areas where bison did not feed for each sample period.

4. Results

4.1. Range production and composition

The annual herbage yield estimated in 1974 and 1975 for wet meadows (4480 and 4320 kg/ha, respectively) was significantly greater ($P < 0.001$) than the yield estimated for dry meadows (2680 and 1880 kg/ha, respectively) (Table 1). The standing dead and litter plant material averaged 2880 kg/ha in 1975 for wet meadows, which was numerically lower than but not significantly different from ($P > 0.05$) the 3120 kg/ha estimated for dry meadows.

Within the main part of the study area (7546 ha), 4803 ha (64% of the area) were classified as meadowland, of which 1083 ha (23% of the meadow area) were classified as wet meadows and 3720 ha (77%) as dry meadows (Reynolds *et al.* 1978).

Wet meadow habitat supported seven major plant groups, which produced 98% of its herbage biomass, and dry meadow habitat supported six major plant groups, which provided 86% of its herbage biomass (Table 2). Slough sedge (*Carex atherodes*), reed grasses (*Calamagrostis* spp.), and beaked sedge (*Carex rostrata*) collectively represented 84% of the total composition of wet meadows, and reed grass and baltic rush (*Juncus balticus*) collectively yielded 77% of the plant biomass of dry meadows. The two most common plants of meadow habitat were slough sedge and reed grasses, which composed 66% of the total meadow habitat (Table 2). Reed grasses represented the greatest proportion of the total meadow biomass (46%), followed by slough sedge (20%).

4.2. Food habits

Bison diets from the SRL contained 29 different plant species, of which 12 species contributed at least 1% each in any one season (Table 3). Slough sedge and reed grasses were the two most abundant food items in the diets of bison in all seasons, ranging from 42 and 35% in winter diets to 77 and 15% in spring diets, respectively. Collectively, they made up 92% of the spring diet, 70% of the summer diet, 79% of the fall diet, and 77% of the winter diet (Reynolds 1976). Other important food items were beaked sedge (1–17%) and willows (1–8%). The rank order of the major plant species selected by bison throughout the year did not change although the actual quantities and number of food items eaten varied. The greatest variety of food items was eaten during summer and the least during winter. The plant composition of bison diets was more like that of wet meadows than that of dry meadows; however, it did not appear to be directly proportional to plant abundance in the habitat.

4.3. Snow cover characteristics

Sample sites were selected in bison feeding areas on the basis of fresh signs of disturbance and cratering. "Non-feeding sites" were not precisely defined, except that evidence of feeding was not detected. Feeding site measurements were obtained from only one feeding area for the November–December and February sample periods, from six feeding areas for the March sample, and from two areas for April. During winter 1974–75, no feeding bison and no signs of bison activity were observed within the designated non-feeding areas. However, both transect areas were used by bison during summer.

Differences in snow characteristics between feeding areas and non-feeding areas were greatest for hardness (Fig. 2). Although snow depths and densities were generally slightly lower on feeding areas compared to non-feeding areas (Table 4), and although some differences were statistically significant, those differences were considerably less than the differences in snow hardness. Within bison feeding areas, the average integrated ram hardnesses for November–December, February, March, and April were 22, 87, 91, and 102 kg-f/cm, respectively. The mean value for November–December was significantly lower ($P < 0.05$) than the means for February, March, and April, which were not significantly different ($P > 0.05$) from each other (Fig. 2). Within non-feeding areas, integrated ram hardness values averaged 216, 247, and 242 kg-f/cm for February, March and April, respectively. These values were not significantly different ($P > 0.05$) from each other.

Table 1
Herbage yield (oven dry weight) for wet and dry meadow types by transects for current annual growth from the Hook Lake vicinity, 1974 and 1975 (Data reprinted from Reynolds *et al.* 1978, p. 585, with permission of the publisher.)

	Wet meadows			Dry meadows		
Year	Transect	*N*	Mean,* ± 2 SE kg/ha	Transect	*N*	Mean,* ± 2 SE kg/ha
1974	1	80	4480[b] ± 240	1	80	2680[c] ± 320
1975	1	40	4840[b] ± 640	1	40	2520[c] ± 280
	2	50	4160[b] ± 400	2	40	1560[d] ± 160
	3	40	3040[a] ± 440	3	40	1640[d] ± 160
	4	40	4800[b] ± 440	4	40	1560[d] ± 120
	5	40	4880[b] ± 360	5	40	2160[c] ± 200
	Total	210	4320 ± 240	Total	200	1880 ± 120

* Within columns, means followed by same letter are not significantly different ($P > 0.05$) by Tukey's multiple comparison test.

Table 2
Average net biomass and percentage composition of plant categories of meadow areas near Hook Lake, 1975 (Data reprinted from Reynolds *et al.* 1978, p. 584 with permission of the publisher.)

	Wet habitat (N = 42)		Dry habitat (N = 40)		Combined meadow habitat†	
Plant species*	Mean, ± 2 SE kg/ha	Percent composition	Mean, ± 2 SE kg/ha	Percent composition	kg/ha	Percent composition
Carex atherodes	2240 ± 700	49	20 ± 20	1	531	20
Calamagrostis spp.	850 ± 460	18	1300 ± 250	64	1196	46
Carex rostrata	760 ± 380	17			175	7
C. aquatilis	190 ± 140	4			44	2
Scholochloa festucacea	210 ± 220	5			48	2
Glyceria spp.	110 ± 90	2			25	1
Moss	140 ± 100	3	70 ± 80	3	86	3
Juncus balticus			270 ± 140	13	208	8
Carex foenea			60 ± 30	3	46	2
C. aenea			40 ± 60	2	31	1
Other‡	40	2	240	14		

* Standard errors were calculated on all species; most common ones are shown above.
† Adjusted plant species' dry weights on basis of 23% wet habitat and 77% dry.
‡ Other species contributing <1% of the total biomass in the wet habitat were *Beckmannia syzigachne, Alopecurus aequalis, Petasites sagittatus, Galium boreale, Ribes oxyacanthoides, Geum aleppicum, Stachys palustris, Polygonum amphibum* var. *stipulaceum*; in the dry habitat, species contributing <1% were *Fragaria virginiana, Rubus acaulis, Aster* spp., *Vicia americana, Epilobium angustifolium, Thalictrum venulosum, Solidago canadensis, Potentilla* spp., *Artemisia biennis, Stellaria* sp., *Achillea millifolium, Hordeum jubatum, Senecio* spp., *Poa* spp., *Viola adunca, Cirsium foliosum, Antennaria rosea, Taraxacum officinale, Lactuca pulchella, Atriplex subspicata, Shepherdia canadensis, Salix* spp., Licben, *Sisyrinchium* sp., *Geum aleppicum, Stachys palustris, Polygonum amphibum* var. *stipulaceum, Agropyron trachycaulum, Puccinellia borealis.*

Comparisons of mean values for integrated ram hardness between feeding areas and non-feeding areas for February, March, and April samples resulted in significant differences ($P < 0.001$). Non-feeding site mean values were significantly greater ($P < 0.05$) by approximately two and one-half times than corresponding average values for feeding sites (Fig. 2).

Within non-feeding areas, the correlation coefficients for snow hardnesses compared to snow densities in each sample period ranged from 0.11 to 0.39 with significant r values of 0.39 and 0.20 ($P < 0.05$) in February and April, respectively. Within feeding areas, the correlation coefficients of snow hardnesses compared to snow densities ranged from − 0.03 to 0.34 with only the February correlation (r = 0.34) being significant ($P < 0.01$).

Differences in mean snow depths between feeding and non-feeding areas were relatively small except during April (Table 4). Average snow depths increased from November to March and decreased in April. Significant differences ($P < 0.001$) in mean snow depth occurred between feeding areas and non-feeding areas in all but the November–December sample period (Table 4). Mean snow depth was less in the feeding areas except for the February sample. The greatest mean snow depth was observed in non-feeding areas in March, and in feeding areas, the greatest mean depth occurred in February.

Mean snow densities increased consistently with time, between November and March, in both feeding and non-feeding areas (Table 4). Mean snow density was less in feeding areas than in non-feeding areas in all but the November–December sample. However, mean values for feeding sites were not significantly different ($P > 0.05$) from non-feeding areas in the February, March, or April sample periods. Mean snow densities did not exceed 0.27 g/cm^3 within feeding or non-feeding sites.

Table 3
Percentages of various food items in bison seasonal diets in 1974 and 1975 (after Reynolds 1976)

Plant category*	Spring	Summer	Fall	Winter
Carex atherodes	77	49	59	42
Calamagrostis spp.	15	21	20	35
Carex rostrata	1	1	6	17
C. aquatilis	2	1	3	2
Salix spp.	2	8	2	1
Juncus balticus	<1	4	3	1
Geum aleppicum	<1	4	4	—
Carex foenea	<1	3	<1	T†
C. aenea	<1	2	<1	—
Equisetum spp. (*arvense,fluviatile*)	<1	T	2	<1
Agropyron trachycaulum	<1	2	<1	<1
Potentilla spp.		3		

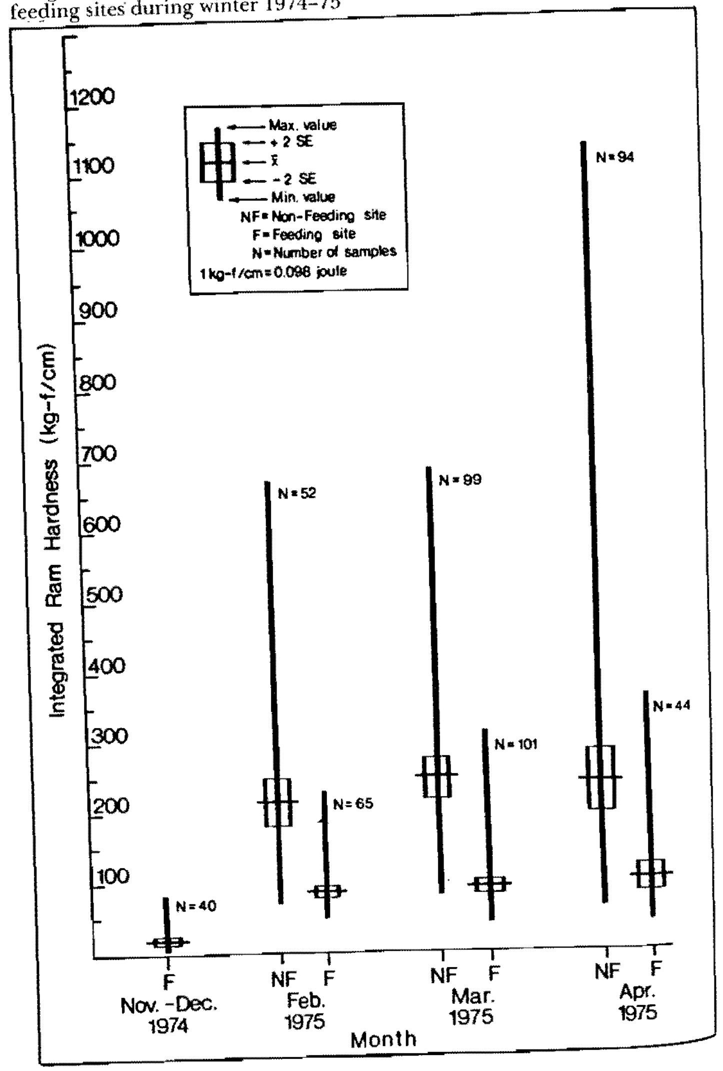
* Other plants that were present in any one season in amounts <1% were *Puccinellia borealis* and *Scolochloa festucacea* (all seasons); *Alopecurus aequalis* (spring and summer); moss (spring and winter); *Glyceria* spp. (summer and fall); *Sparganium multipedunculatum* (summer and winter); *Scirpus validus* (winter); *Beckmannia syzigachne, Agrostis scabra, Stachys palustris, Hordeum jubatum, Atriplex subspicata, Fragaria virginiana, Vicia* sp., *Lathyrus* sp., *Shepherdia canadensis*, and *Picea glauca* (summer); and unidentified forbs (spring, summer, fall).
† T = Trace amount.

Table 4
Mean snow depth and density measurements for bison feeding sites and non-feeding sites during winter 1974–75.

Month and type of site	Sample size	Mean* ± 2 SE depth, cm (range)	Sample size	Mean* ± 2 SE density, g/cm^3 (range)
November–December (1974)				
Feeding	152	27^{ab} ± 0.8 (13–43)	65	0.14^{b} ± 0.014 (0.03–0.26)
Non-feeding	161	30^{b} ± 1.8 (4–57)	42	0.12^{a} ± 0.016 (0.02–0.20)
February (1975)				
Feeding	130	57^{e} ± 1.4 (40–100)	65	0.15^{bc} ± 0.006 (0.10–0.22)
Non-feeding	201	53^{d} ± 1.4 (32–100)	50	0.18^{cd} ± 0.012 (0.11–0.26)
March (1975)				
Feeding	220	55de ± 1.1 (33–83)	120	0.18^{d} ± 0.004 (0.11–0.24)
Non-feeding	200	60^{f} ± 1.4 (41–107)	100	0.19^{d} ± 0.008 (0.09–0.27)
April (1975)				
Feeding	75	24^{a} ± 1.1 (14–40)	44	0.25^{e} ± 0.014 (0.14–0.36)
Non-feeding	200	40^{c} ± 2.0 (18–117)	100	0.27^{e} ± 0.01 (0.14–0.39)

* Within each column, means followed by the same letter are not significantly ($P > 0.05$) different as determined by Tukey's multiple comparison test.

Figure 2
Integrated ram hardness values of snow for bison feeding sites and non-feeding sites during winter 1974–75



5. Discussion

5.1. Range production

Wet meadow habitat produced, on the average, from 1.5 to 2 times as much plant biomass as did dry meadow habitat during both years of the study. The herbage production of northern meadows in the SRL exceeds that of southern rangelands (Peden 1972, Telfer and Scotter 1975). That high level of vegetative production is part of the reason why so much interest has been expressed in the grazing potential of the area. Although in this study the annual variation in plant biomass production was small between years (1974 and 1975), other studies have shown that mean annual estimates of plant biomass in northern rangelands can vary as much as 50% (Pringle, this publication; Bailey and Penner 1973). Wet meadows had higher production and lower variation than dry meadows, which suggests that range management should be directed towards the wet meadow type to achieve maximum carrying capacity for bison.

The quantity of dead plant matter on both meadow types, especially on the dry meadow, indicated a low level of grazing relative to production and may have inhibited plant growth. Yields might be stimulated by prescribed burning. In Alaska, the Farewell bison herd appeared to be expanding its winter range because of fire-related habitat changes that caused an increased area of sedge-grasslands contiguous with summer and pre-fire winter ranges (Campbell and Hinkes 1983). Increased grazing intensity and more efficient range use by bison under post-fire conditions would likely cause an increase in herbage production through reduction of carryover of dead plant matter. Fire is a potential tool for use in range manipulation to aid in management of northern bison populations.

5.2. Food habits[1]

In most situations North American bison are grazers. Because bison habitats vary widely, it is useful to identify bison diets by association with geographic areas. Table 5 compares seasonal diets from four different populations of bison by forage class. Grasses and sedges were the most important foods of free-roaming bison in three of those herds.

In the Northwest Territories, bison habitat along the SRL is within the boreal forest region of Canada where white spruce (*Picea glauca*) forests separate vast open meadows supporting sedge and grass communities. Slough sedge was by far the most abundant plant in the diet, varying from 42% in winter to 77% in spring. The second most common food was reed grass, which varied from 15% of the diet in spring to 35% in winter. These two forages contributed more than 70% of the bison diet in 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, they composed 66% of the plant biomass of the total meadow habitat and were the two most abundant meadow plants in the SRL. Forbs and browse appeared to be of minor importance and were consumed mainly in summer and fall.

5.2.1. Forage selection — Bison generally are less selective in what they eat than other ungulates under similar environmental conditions. In the Henry Mountains of Utah, bison and cattle selected similar forage, but bison tended to move more, did not overgraze preferred feeding areas, and made greater use of steep slopes (Nelson 1965). Thus, bison used their range more uniformly with less damage to forage species. A high degree of overlap (91% similarity) between diets of bison and cattle was reported in fall 1980 on a seeded range (Van Vuren and Bray 1983), but diets of both species, as determined by fecal analysis, were related to forage availability. The diets of bison on the shortgrass plains of Colorado resembled cattle diets more than sheep diets in areas of light grazing (Peden 1972). Bison were less selective than cattle and are, therefore, better adapted to use the herbage resource of the shortgrass prairie more fully (Peden *et al.* 1974). In Yellowstone National Park, forage availability appeared to regulate bison feeding patterns within the preferred sedge and upland feeding sites (Meagher 1973). Bison were usually the least selective and cattle the most selective during feeding trials involving bison, yak, and cattle when sedge, grass, and alfalfa hays were provided (Richmond *et al.* 1977). In northern Canada, forage consumption by bison was not directly proportional to plant availability, indicating light to moderate feeding selection (Reynolds *et al.* 1978). 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 are usually associated with plant phenology in favour of new growth herbage.

Bison digest poor quality feed better than cattle do (Hawley, this publication). Based on the results of forage selection trials from several range types, bison appear better adapted than cattle to use the herbage resource of the SRL efficiently. In addition, bison are better adapted than cattle to survive harsh winter conditions and the severe environment of northern rangelands (Hawley, this publication).

[1] Data in this section are reprinted from Reynolds *et al.* (1982), pp. 985-986, with permission of the publisher.

Table 5
Percentage composition in the diet of bison by forage class and season as summarized from four studies in different range types (Reprinted from Reynolds *et al.* 1982, p. 985 with permission of the publisher.)

	Season and locality*															
	Winter				Spring				Summer				Fall			
Forage class	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Grass	34	87	36	27	46	79	16	57	32	88	24	72	30	89	21	57
Sedge and rush	65	†	63	†	50	16	81	1	59	1	59	4	69	—	71	2
Forbs	†	9	—	3	3	†	1	17	6	3	8	7	†	9	4	11
Browse	1	—	1	67	†	—	2	25	2	—	8	17	†	—	2	29

* A: Yellowstone National Park — forested, with interspersed grass–sedge meadows (after Meagher 1973).
B: Northeastern Colorado — shortgrass plains (after Peden 1976).
C: Northern Canada — boreal forest interspersed with large grass–sedge meadows (after Reynolds 1976).
D: Colorado National Monument — semi-desert range, southwestern Colorado. Average of samples collected from three canyons (after Wasser 1977).
† Less than 1%.

5.3 Snow cover characteristics

Integrated ram hardness is assumed to be an index of work required by an animal to dig through a snow layer. However, the type of force that an animal will exert in moving through snow may be different from that of the conical penetrometer (Lent and Knutson 1971). Lent and Knutson (1971) reported integrated ram hardness values in excess of 3000 kg·f/cm for snow in the interior of Nunivak Island in Alaska but a mean value of only 133 kg·f/cm on muskox feeding sites along the coast. Bison occupying the SRL used winter feeding sites where integrated hardness of snow was approximately 40% as great as integrated hardness in areas not used for feeding. Our data are not sufficient to determine what integrated ram hardness values would prevent bison from feeding, but we observed that mean values up to 105 kg·f/cm did not seriously affect the ability of bison to make feeding craters by head swinging. We noted no other methods of foraging by bison. If snow hardness had limited foraging, the effect would have existed from early February to late April because snow hardness did not differ significantly between sample periods. Pruitt (1959) reported that snow hardness had a greater influence than density on the distribution of barren-ground caribou (*Rangifer tarandus*). Similarly, snow hardness in the SRL appeared to influence selection of feeding sites by bison more than either depth or density.

In the Pelican Valley of Yellowstone National Park, bison were able to feed through average snow depths of 102–114 cm, but a shift to areas of less snow cover occurred when snow depth exceeded 127 cm (Meagher 1971). In Elk Island National Park, bison moved through deep snow by travelling on trails in single file. Within bison feeding areas in the park, mean snow depths for January and February 1974 ranged from 57 to 70 cm and from 47 to 70 cm in non-feeding areas (Van Camp 1975). Van Camp concluded that undisturbed snow deeper than 50–60 cm can impede the movement of bison calves and that depths of 65–70 cm can impede the movements of mature bison. Mean snow depths on the SRL during winter 1974–75 did not appear to limit feeding or movement of mature bison (Table 4). Snow cover in February and March (mean depth 53–60 cm) was deep enough to curtail extensive movements by calves. That was not observed to be a problem for the few herds travelling in the southeast part of the study area. However, a major portion of the Hook Lake herd wintered south of the study area where ground access was limited. Snow conditions there may have been less severe than in the areas where measurements were taken.

A few studies have investigated the effects of snow density on movements of wintering ungulate populations. Kelsall and Prescott (1971) reported that low snow density (0.10–0.19) did not support ungulates (mean track depth was 88% of the mean snow depth), snow density in the range of 0.20–0.29 provided some support (mean track depth was 76% of the mean snow depth), densities of 0.30–0.39 provided more support (mean track depth was 57% of the mean snow depth), and densities of 0.39–0.49 provided good support (mean track depth was only 47% of the mean snow depth). The threshold of sensitivity to snow density for barren-ground caribou appeared to be 0.20 within feeding areas and that for locomotion within resting areas appeared to be between 0.25 and 0.30 (Pruitt 1959). In Elk Island National Park, when snow densities reached 0.18–0.21, bison calves abandoned the normal head swing mode of feeding. However, at densities of 0.25, adult animals were still able to clear snow effectively with head swing behaviour (Van Camp 1975). Mean snow densities recorded in the SRL during winter 1974–75 did not appear to curtail feeding or movement of mature bison. Our results suggested that, of the periods considered, only late winter (April) snow densities, which were directly related to spring thaw, would have presented problems to foraging bison (Table 4). Again mainly calves would have been affected.

Density measurements from the SRL did not correlate well with hardness. Consequently, we believe that it is not possible to accurately predict values for ram hardness from the more easily taken density measurements, at least within the range of our data. Snow hardness must be measured independently of other snow parameters. The Rammsonde penetrometer appears to be an efficient means of obtaining an index of snow hardness for ecological studies.

Telfer and Kelsall (1979, 1984) used measurements for chest heights and weight loads on track to estimate capabilities of several animal species to cope with snow. Among bison, moose, wapiti, and white-tailed deer, bison were the least adapted to deep snow based on those measurements. Nevertheless, in a year of greater than average snowfall in the SRL, snow depth and density did not appear to limit movements or feeding ability of adult bison, although they may have been a problem for calves and yearlings. Bison and white-tailed deer adapt behaviourally to deep, dense snow by following old trails and maintaining beaten paths (Van Camp 1975, Telfer and Kelsall 1979) and thereby save energy (Telfer and Kelsall 1984). In their comparative study of snow-coping ability of 11 North American mammals, Telfer and Kelsall (1984) calculated lower index values for wapiti and bison than for their predators, which suggests that both species should be relatively easy prey for wolves in winter.

Differences in snow depth and density between areas in the SRL appeared to have had a minor influence on bison distribution and their selection of feeding sites. Hardness and density measurements were not closely related, and we suspect that of the three parameters measured, hardness was the most important influence on bison use of feeding areas. Bison will choose areas of soft snow for winter feeding habitat and will avoid large open and wind-swept meadow areas. In the SRL, snow hardness appeared to be the most critical factor influencing food selection by bison during the period of snow cover in 1974–75.

6. Conclusions

Herbage production levels and quantity of forage did not restrict the bison population in the SRL. Slough sedge and reed grass were the two most common plants in the diets of bison and the two most abundant plants in the SRL. Range management should, therefore, focus on increasing production in communities dominated by these species. Increased herbage production may be possible by the use of prescribed burning to decrease the amount of carryover.

Based on the results of snow measurements taken in the SRL during winter 1974–75, snow depths and densities did not limit movements or feeding of adult bison; snow hardness was likely the factor most influencing selection of feeding sites by bison. Late winter snow depth and density measurements approached critical levels for calves and yearlings and may have restricted their movements and feeding.

Seasonal variation in forage quality

Hal W. Reynolds
Alexander W.L. Hawley

1. Abstract

Range plants, collected on the Slave River lowlands (SRL) from July 1974 through August 1975, were analysed to determine seasonal variation in nutrient composition of a hay mixture from each of wet and dry meadows. The nutritive quality of native vegetation in the SRL was highest in June and was generally higher in hay from wet meadows throughout the year, except during June. Wet meadows would constitute a better source of hay. Crude protein (CP) contents were highest in June, with values of 13.4 and 11.8% in hay samples from dry and wet meadows, respectively. Wet meadows had higher levels of CP than dry meadows, except during June. CP contents declined rapidly after July. Native vegetation in the SRL would yield hay of adequate quality for beef cattle if harvested in June or July. The highest quality of native hay would be obtained by harvesting in June; however, wet meadows are often difficult to harvest then and yield would not be as great as in July or August. The best compromise between forage quality, yield, and the technical difficulty of cutting hay on wet sites would be to harvest hay in July.

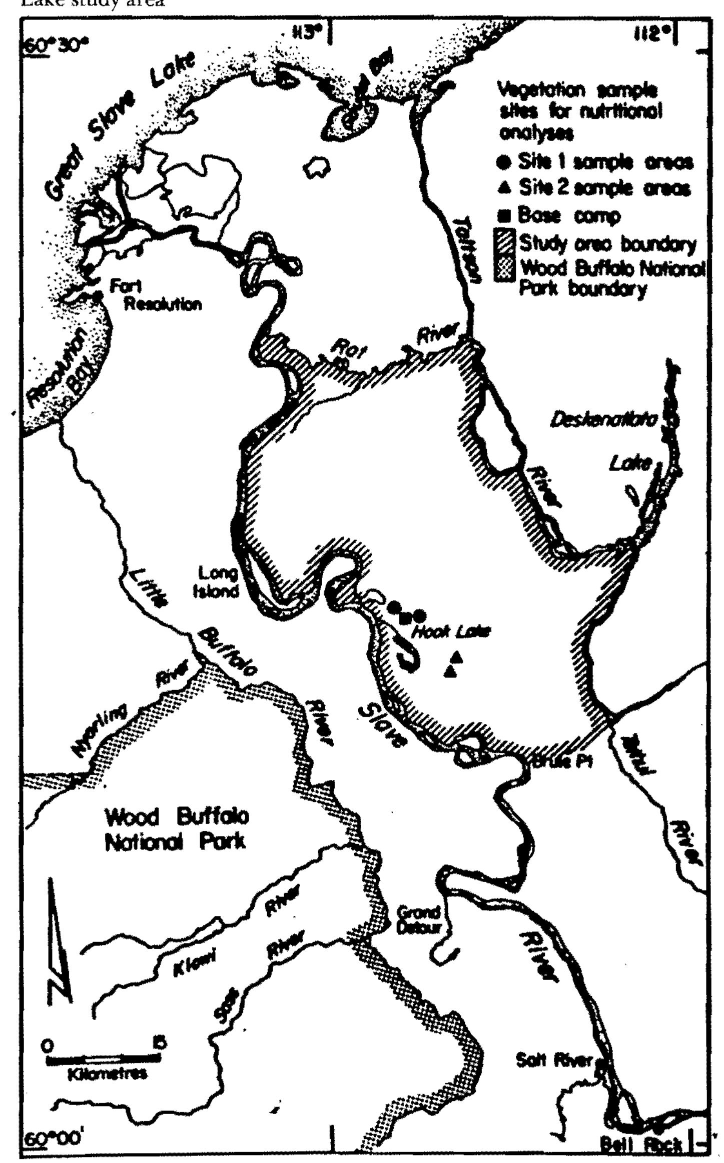
2. Introduction

An evaluation of the Slave River lowlands (SRL) as rangeland for bison and cattle was initiated because of public interest in obtaining grazing leases for domestic livestock in the area. That evaluation included assessments of biomass production and quality of range vegetation in the Grand Detour and Hook Lake areas. The best rangeland for grazing in the SRL comprises scattered wet and dry meadows, which cover about 33% of the total area (Day 1972). Meadows in the Hook Lake region are composed of 77% dry meadows, which are dominated by grasses, and 23% wet meadows, which are dominated by sedges (Reynolds *et al.* 1978). Yield and species composition of vegetation on SRL ranges have been reported (Reynolds 1976; Reynolds *et al.* 1978; Reynolds and Peden, this publication; Pringle, this publication). This paper describes nutrient composition and quality of meadow hays harvested from wet and dry meadows and discusses strategies for cutting hay in relation to seasonal changes in hay quality in the Hook Lake area of the SRL.

3. Methods

Chemical analyses to determine nutrient contents were conducted on range plants collected at eight different times between July 1974 and August 1975 from each of two sites representing wet and dry meadow vegetation. Site 1 consisted of two areas, of about 2 ha each, within a 2-km radius of the Hook Lake base camp. Samples from site 2 were collected within two areas of similar size centered 12 km farther south (Fig. 1). Sample dates were represented by the mid-points of each collection period, namely, 20 July (samples collected 18–22 July, 1974), 28 September

Figure 1
Vegetation sample collection sites for nutritional analyses in the Hook Lake study area



(28 September 1974), 6 December (2–10 December 1974), 9 February (8–10 February 1975), 17 March (14–19 March 1975), 19 April (18–20 April 1975), 27 June (22 June–3 July 1975), and 12 August (12 August 1975). No distinction was made between years of collection.

The current year's growth of individual plants of all species was clipped at approximately 3 cm above ground or water level. Both vegetative and reproductive parts of plants were collected in samples in a mixture representative of their proportions in that area. Entire plants were bagged separately by species, air dried in the field, oven dried in the lab at 50–60°C for 48 h, and ground through a 1-mm mesh screen in a Wiley mill. Ground plant samples were pooled between sites within a meadow type and analysed by the Alberta Soil and Feed Testing Laboratory, Edmonton, Alberta, to determine the levels of moisture, crude protein (CP), crude fibre (CF), calcium (Ca), and phosphorus (P). Data have been presented on a moisture-free basis. Total digestible nutrients (TDN), an index of available energy, was calculated using the formula TDN = 50.41 + 1.04 CP% − 0.07 CF% (Adams 1975).

Ten plant species were sampled. Eight of them constituted 94% of the biomass in wet meadows; five constituted 80% of the biomass in dry meadows (Table 1). Three plant species in wet meadows and two in dry meadows occurred in trace amounts and each was assigned a representative 1% of the biomass for this analysis (Table 1).

We calculated the nutrient composition of hay weighted for each of wet and dry meadows using the nutrient composition of each species, the proportional representation of each in wet and dry meadows, and the proportion of wet and dry meadows in the SRL. Differences in the net nutrient composition of the hay samples from wet and dry meadows reflected differences in the proportions of plant species occurring in each type of meadow. We averaged nutrient values between plant collection sites within meadow types and used the average to calculate the weighted nutrient composition value for each meadow type. Chemical constituents were tested for linear correlations.

4. Results

The weighted calculations for the combined meadow habitat favoured dry meadows because 77% of the meadow habitat in the Hook Lake area is dry meadow. The percentage biomass data in Table 1 for each plant species was used to calculate the weighted nutrient composition.

Nutrient composition varied greatly among seasons; however, the most pronounced changes occurred between April and October (Fig. 2). There were higher levels of all nutrients except CF in vegetation from wet meadows than from dry meadows, except in the June sample. Differences between meadows were greatest for Ca and TDN. Crude fibre was much lower in wet meadow vegetation except for the June sample when values were equal for both meadow types.

The CP content of samples was highest in late June. Dry meadows had a weighted CP content of 13.4% and wet meadows 11.8% at that time, which was the only sample date when dry meadows exceeded wet meadows in CP content. Levels of CP declined rapidly in July and gradually throughout the winter to a minimum of approximately 3% in April in both types of meadows (Fig. 2). There was little change in CP content of meadow vegetation from December through April.

Crude fibre followed an inverse seasonal cycle compared to CP and the levels of CP and CF were significantly and inversely correlated ($P < 0.001$, $r^2 = 0.83$, $N = 16$). Both meadows had CF contents of about 37% in late June. The CF content of dry meadow vegetation increased sharply by approximately 8% from June to July, whereas the CF content of wet meadow vegetation rose less than 1% during that time (Fig. 2). The difference in CF content between wet and dry meadows was greatest in July samples. When values of both meadow types were pooled to represent a combined meadow, CF content increased by approximately 6% from June to August. The CF content increased slightly throughout the winter in both meadow types to the seasonal maximum of about 51% in April. There was little change in CF content between October and April. Wet meadow herbage had a lower CF content than herbage from dry meadows on all sampling dates, except in June (Fig. 2).

Seasonal variation in TDN paralleled that of CP (Fig. 2). The TDN level was highest in late June and was higher in vegetation from wet meadows than in that from dry meadows, except for the June sample. There were no major seasonal differences in TDN from December to April.

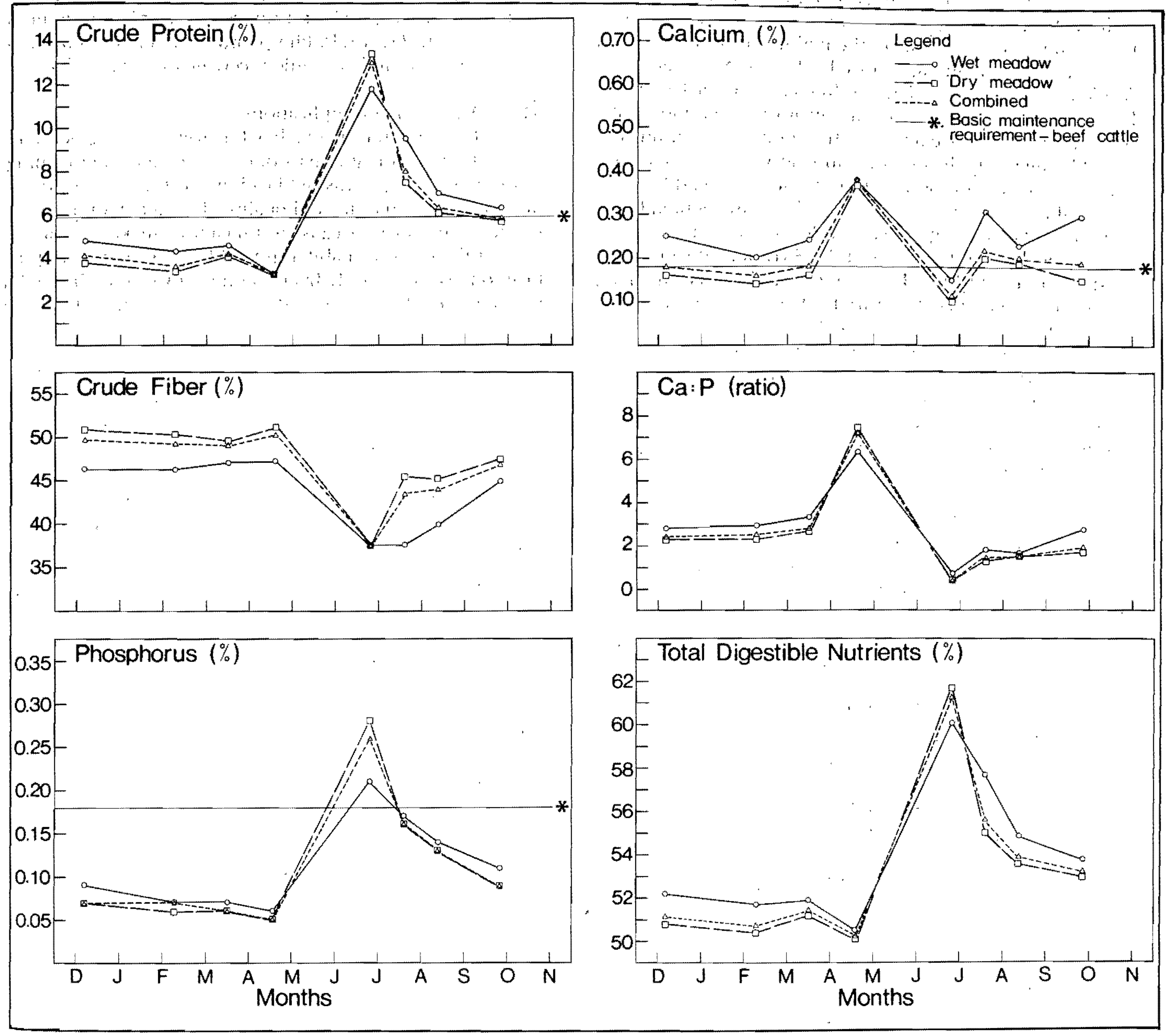
Simultaneous peaks in Ca content occurred in both meadow types in April (about 0.4% Ca) and July (0.2 to 0.3% Ca) (Fig. 2). Calcium levels were higher in April and July than at other times of the year. In contrast, P levels displayed a single seasonal peak of between 0.2 and 0.3% in late June. Phosphorus levels differed little from October to April. Both Ca and P contents were consistently higher in wet meadows than in dry meadows except for P levels in June. The Ca:P ratio also showed a seasonal cycle and varied from less than one in late June to an annual peak of about seven in late April. Phosphorus and Ca levels were not significantly correlated but the level of P was highly correlated ($P < 0.0001$, $r^2 = 0.96$, $N = 16$) with CP content.

Table 1
Plant species collected for nutrient analyses during eight collection periods from July 1974 to August 1975 and the percent composition of the dry matter biomass of those species in each of wet and dry meadow habitats*

Plant species	Wet meadows (23% of SRL meadows)		Dry meadows (77% of SRL meadows)	
	Percent of biomass	Number of sample periods represented	Percent of biomass	Number of sample periods represented
Carex atherodes	49	8	1	8
Calamagrostis spp.	18	8	64	8
Carex rostrata	17	7†		
Scolochloa festucacea	5	8		
Glyceria spp.	2	7‡		
Geum aleppicum	1	8	1	8
Beckmannia syzigachne	1	7†		
Rumex occidentalis	1	6§		
Juncus balticus			13	8
Agropyron trachycaulum			1	8

* Data from Reynolds 1976; Reynolds *et al.* 1978.
† July 20 not represented.
‡ February 9 not represented.
§ July 20 and September 28 not represented.

Figure 2
Weighted values for chemical composition of hay from wet and dry meadows in the Slave River lowlands



5. Discussion

5.1. Forage quality

The quality of native vegetation in the SRL was best in late June when vegetation from both meadow types was highest in CP, TDN, and P and lowest in CF. The high Ca:P ratio in late April did not exceed recommended levels for beef cattle feed (National Academy of Sciences – National Research Council 1976). We cannot say whether the exact seasonal peak in forage quality coincided with the sampling date in late June because of the rapidity of phenological changes in plants during the growing season and because we pooled data from 2 years.

Wet meadow vegetation was more nutritious than that from dry meadows except during late June. Because sedges predominate in wet meadows and grasses in dry meadows, the nutritive differences between meadow types are likely related to differences between the two plant groups: sedges from the Hook Lake area tend to be higher in CP, Ca, and P and lower in CF than grasses throughout the year except in June (H. Reynolds, unpubl. data). This is likely the result of differences in phenological development between grasses and sedges. Thus, wet meadows, because of their superior yield and quality, would constitute a better source of hay and would be better suited for year-round grazing than dry meadows (Reynolds and Peden, this publication; Pringle, this publication). Indeed, free-ranging bison in the SRL and in other areas prefer sedge meadows over grass meadows (Reynolds and Peden, this publication).

The CP in hay harvested from wet and dry meadows in June, July, and August, and from wet meadows in September was adequate to meet the maintenance requirement (5.9%) for dry, pregnant, mature beef cows (National Academy of Sciences – National Research Council 1976). However, gestation, lactation, and growth requirements of cows and maintenance and growth requirements of bulls would be met only during June and early July. The CP content of hay from both wet and dry meadows would be marginal for most classes of beef cattle during September and inadequate during the remainder of the year.

The TDN in forage from the SRL ranged from 50% in April to 61% in June (Fig. 2) and would exceed the maintenance requirements of mature beef cows during June, July, August, and September (National Academy of Sciences – National Research Council 1976). During the gestation period of beef cattle (approximately September to May), native vegetation would exceed the basic maintenance requirement only in September. The TDN needed for growth and maintenance of young beef cattle and adult bulls would only be supplied by native hay if it were harvested during June and July.

Native hay in the Hook Lake area would not meet the basic requirements of free-ranging beef cattle for protein and energy except during June, July, and August but hay would be of adequate quality if harvested in June or, less ideally, in July.

Levels of CP and energy that are inadequate for cattle are not necessarily inadequate for free-ranging bison. Bison were more efficient than beef cattle in digestion of feed when diets were relatively low in CP and high in fibre (Peden *et al.* 1974; Richmond *et al.* 1977; Hawley, this publication). Bison may have a more conservative nitrogen balance than cattle. In addition, bison may have an inherent seasonal metabolic adjustment that allows them to minimize nutrient requirements during winter when forage quality is low, and maximize growth and production in summer when forage quality is high (Hawley, this publication). Furthermore, free-ranging animals are not constrained to consumption of entire plants. Wild bison tend to select the leafy tops of many plant species, which are higher in nutritive quality than the lower parts of the same plants (H. Reynolds, unpubl. data).

The Ca content of vegetation from wet meadows in the SRL appeared to meet the 0.18% maintenance requirement (National Academy of Sciences – National Research Council 1976) for most classes of beef cattle in all seasons except during peak growth in June (Fig. 2). Dry meadow vegetation was inadequate in Ca content in June and marginal or inadequate in September, December, February, and March. The low level of Ca in dry meadow vegetation reflected the lower level of Ca in grasses than in sedges. The Ca peaks in April and July suggest a biphasic seasonal cycle (Fig. 2). The low Ca:P ratio in June could exacerbate Ca deficiencies then.

The high correlation between P and CP contents may have been related to a high proportion of phosphoproteins in the vegetation. The P content of wet and dry meadow vegetation was adequate to meet the maintenance requirements (0.18%) for dry, pregnant, mature beef cows (National Academy of Sciences – National Research Council 1976) only in June. Deficient levels of P in the vegetation of the SRL were also reported for the Grand Detour area (Pringle, this publication). Phosphorus deficiency in native vegetation is widespread, and P is usually one of the most limiting nutrients for ruminants; inadequate supplies of P can disrupt Ca deposition in and removal from bone, can decrease Ca absorption, and can reduce fertility in domestic cattle (Church *et al.* 1971). Phosphorus would have to be given as a supplement to beef cattle receiving only native hay.

5.2. Management implications

Production of native hay for overwintering beef cattle would be an integral part of commercial cattle ranching in the SRL (Pringle, this publication). Wet meadows produce a greater quantity and quality of forage than do dry meadows; however, because wet meadows make up only 23% of the meadow habitat in the SRL, it would be impractical to harvest hay only from wet meadows. In addition, for maximum quality of hay in the SRL, the optimum time to harvest is during late June, but wet meadows may be difficult to harvest then. In June, levels of CP and P in plants collected from dry meadows were higher than in plants collected from wet meadows. Therefore, hay cut from dry meadows in June would be superior in quality to hay cut from wet meadows in June. However, hay prepared in June from either meadow type would be inadequate in Ca content. Hay harvested at any time other than June should be cut from wet meadow vegetation, if it is to be of the highest quality. The best harvest strategy would be to cut hay from wet meadows during mid to late July when CP levels are still well above maintenance levels, the CF content has changed little from the minimum level in June, Ca content is adequate to meet the maintenance requirements for most classes of beef cattle, and P levels, although marginal, are at their second highest annual level. Harvesting in July would not provide the highest quality hay but would represent the best compromise between forage quality and yield and the technical difficulty of harvesting hay from wet sites. Hay from combined meadows would be inferior in quality to hay harvested solely in wet meadows.

Bison and cattle use of forages

Alexander W.L. Hawley

1. Abstract

North American bison (*Bison bison*) digested forages native to the Slave River lowlands more efficiently than did Hereford cattle (*Bos taurus*). Average daily weight gain and feed conversion rates were greater for bison steers than for cattle steers when slough sedge (*Carex atherodes*) hay was fed in summer. In winter, bison decreased intake of sedge to a maintenance level, and average daily gain and feed conversion were greater for Hereford steers. Hereford steer calves also exceeded bison steer calves in gain and feed conversion when a ration exceeding the maintenance requirements of cattle was fed to both species. Physiological differences between bison and cattle in their extraction and use of nutrients were reflected in differences in blood composition.

2. Introduction

The Slave River lowlands (SRL) constitute an important range for bison (*Bison bison*) and might be suitable as rangeland for cattle (*Bos taurus*). To evaluate the range's potential for those species we need to compare their abilities to digest native forages. Peden *et al.* (1974) and Richmond *et al.* (1977) compared digestive efficiencies of bison and cattle, but forages from the SRL and other northern ranges were not tested. Few data are available for extrapolation to SRL forages. The experiments reported here were conducted to compare the use of SRL forages by bison and cattle. Dry matter digestibilities of hay and individual forage species were compared in nylon bag microdigestion experiments. Slough sedge (*Carex atherodes*), one of the most abundant forages in the SRL, was tested in total fecal collection experiments to compare the digestibilities of individual nutrients. Data on animal growth and intake were also collected. Experiments were conducted to determine the change in blood composition with changes in ration composition to evaluate specific differences between cattle and bison in nutrient extraction and use.

3. Methods

3.1. Nylon bag experiments

Nylon bag digestibility experiments were conducted with two bison cows and one Hereford steer receiving a hay ration and two bison (1 steer, 1 cow) and one Hereford cow receiving hay plus a pelleted grain supplement (Hawley *et al.* 1981*a*). Both hay and supplement were fed *ad libitum*. Hay samples were collected from the SRL in early August 1975 from wet and dry meadows. Samples of slough sedge, willow (*Salix* spp.), northern reed grass (*Calamagrostis inexpansa*), baltic rush (*Juncus balticus*), and aleppo avens (*Geum aleppicum*) were collected in February and June of 1975. Digestibilities of hay and individual plant species were compared by measuring dry matter disappearance (DMD) of forage samples from within nylon bags following 48 h incubation in the rumen. Data were analysed using analyses of variance.

3.2. Fecal collection experiments

Total fecal collection digestibility trials were conducted with six yearling bison steers and six yearling Hereford steers (Hawley *et al.* 1981*b*). The digestion of sedge hay was measured for each animal species in each of summer (June–July) and winter (December–January). The test hay, consisting primarily of slough sedge, was harvested near Saskatoon, Saskatchewan, and was coarsely chopped for use in the summer trial and finely chopped for use in the winter trial. Mean dry matter intake as a percentage of body weight was determined for each animal species in each summer and winter season. Digestibility data were analysed using analyses of variance. Body weights were measured daily and average daily gain (ADG) was calculated by linear regression with the effect of gut fill, as represented by daily feed intake, held constant.

3.3. Calf growth and performance

The plains bison used in fecal collection experiments were obtained from Elk Island National Park, Alberta, in September 1975. The cattle were obtained in spring 1976. All animals were fed a formulated ration containing 12% crude protein (CP), 68% total digestible nutrients (TDN), and mineral supplements *ad libitum* whenever digestion or other experiments were not in progress. Body weights were recorded approximately weekly for bison and biweekly for cattle when this ration was fed. Feed intake was recorded daily on a herd basis and the data were used to calculate dry matter intake rates (kg/animal/day). Average daily weight gains were calculated and compared between species by linear regression methods.

3.4. Blood experiments

Hawley and Peden (1982) fed rations containing high protein–high energy, high protein–low energy, low protein–high energy, or low protein–low energy to bison and Hereford steers to determine the response of selected blood components to varying protein and energy levels in the ration. Four blood samples were taken every second day from the jugular vein of each animal during summer and winter trials and the levels of 20 blood components were measured in each sample. The effects of ration protein and energy levels, animal species, and season on blood components were evaluated using analyses of variance.

4. Results

4.1. Nylon bag experiments

The DMD values were consistently and significantly ($P < 0.001$) higher for bison than for cattle (Tables 1 and 2). Site of harvest of hay samples did not significantly affect DMD (Table 1). However, DMD varied significantly among plant species (Table 2). Ration effects were discussed by Hawley *et al.* (1981*a*) and will not be considered here.

Winter samples had lower overall mean DMD values than summer samples for all plant species when results were averaged for both cattle and bison (Table 3). The animal species and the season of harvest interaction was not significant ($P > 0.05$). The effect of season on DMD was greatest for northern reed grass and aleppo avens and least for willow (Table 3). Summer samples differed only slightly in DMD, although slough sedge and aleppo avens were more digestible ($P < 0.05$) than other species. Willow had the greatest mean DMD among winter samples, followed by slough sedge and baltic rush. Northern reed grass and aleppo avens had the lowest winter mean DMDs.

There were significant ($P < 0.001$) interactions between animal and plant species and between plant species and season of collection on DMD. Differences among plant digestibilities were greater in winter than in summer (Table 3) and were greater in cattle than in bison. Winter willow samples had an outstandingly high (49%) digestibility compared with other winter samples when tested in cattle. Sedge and willow had relatively high digestibilities in both seasons and in both animal species. Summer samples of aleppo avens were significantly more digestible than other summer samples when tested in cattle but there were no significant differences ($P > 0.05$) among summer forages tested in bison (Hawley *et al.* 1981*a*).

Winter samples had higher crude fibre (CF) contents than summer samples for all forages except willow (Hawley *et al.* 1981*a*). The percentage seasonal reduction in DMD in winter versus summer samples (Table 3) was highly correlated ($r^2 = 0.81$) with the percentage increase in CF content of winter samples.

4.2. Fecal collection experiments

The sedge hay tested in the fecal collection digestibility trials contained approximately 8.1% CP and 46.5% acid detergent fibre and was comparable in composition to sedge collected in the SRL. Energy, protein, and fibre were digested significantly more ($P < 0.05$) in bison than in cattle. Those nutrients generally showed greater overall digestibilities in the winter trial than in the summer trial (Table 4).

Table 1
Dry matter disappearance (DMD) of hay samples harvested from wet and dry meadows and tested in bison and cattle

		DMD, %	
Variable	Category	Mean ± SE	N
Animal species	Bison	52 ± 1.3*	16
	Cattle	43 ± 1.7	6
Meadow type	Wet	50 ± 1.8	11
	Dry	49 ± 2.1	11

* Means were statistically significantly different ($P < 0.001$) between animal species but were not different ($P > 0.05$) between meadow types.

The interaction between animal species and season on digestibility was significant ($P < 0.05$) only for CP; the increase in CP digestibility in winter was greater in cattle than in bison, although CP digestibility was still numerically greater in bison in winter.

Bison and cattle did not differ significantly ($P > 0.05$) in their average daily intake of dry matter (DM) during the summer trial (Table 4). Cattle DM intake was significantly greater than that for bison during the winter trial. Intake of digestible energy (DE) was numerically but not significantly less ($P > 0.05$) for bison than cattle in winter. There was no significant seasonal difference in bison intake of DM ($P > 0.05$), but cattle consumed significantly more ($P < 0.01$) feed DM and DE in winter than in summer. ADG was significantly greater ($P < 0.05$) for bison than cattle during the summer trial (Table 4). Cattle ADG was numerically greater than bison ADG during the winter trial. Within the cattle, ADG was numerically greater in the winter than in the summer trial. However, those differences were not significant ($P > 0.05$). In contrast, ADG for bison was significantly lower ($P < 0.05$) in the winter than in the summer trial. When compared between the two species, feed conversion was greater for bison during the summer trial and greater for cattle during the winter trial. Bison feed conversion decreased markedly from summer to winter whereas cattle feed conversion increased during the winter trial (Table 4).

4.3. Calf growth and performance

The ADG was significantly greater for Hereford calves than for bison calves when a high quality ration was fed. The maximum rates of weight gain, at 4–18 months of age, were displayed by both species during March–June 1976, inclusive. The ADG during that time was greater for cattle than for bison even when the greater initial weight of cattle was considered (Table 5). Feed conversion was higher for cattle and mean DM intake was significantly lower for bison (Table 5).

Table 2
Dry matter disappearance (DMD) of forage harvested in two seasons and tested in bison and cattle*

		DMD, %	
Variable	Category	Mean ± SE	N
Animal species	Bison	52 ± 2.0†	60
	Cattle	39 ± 2.9	40
Season	Summer	58 ± 1.6†	50
	Winter	35 ± 2.1	50
Plant species	*Carex atherodes*	50[b‡] ± 3.9†	20
	Salix spp.	56[a] ± 1.1	20
	Calamagrostis inexpansa	39[c] ± 4.7	20
	Juncus balticus	47[c] ± 3.4	20
	Geum aleppicum	44[d] ± 4.8	20

* Data from Hawley *et al.* (1981*a*).
† Means were statistically significantly different ($P < 0.001$) within variables.
‡ Plant species means followed by different superscript letters were statistically significantly different ($P < 0.05$) (Student-Newman-Keuls range test).

Table 3
Overall mean dry matter disappearance (DMD) of forages collected in two seasons*

	DMD, %		
	Summer	Winter	
Plant species	Mean ± SE†	Mean ± SE†	Seasonal reduction, %
Carex atherodes	60[ab‡] ± 4.1	40[b‡] ± 4.9	33
Salix spp.	59[b] ± 1.2	52[a] ± 1.2	11
Calamagrostis inexpansa	57[b] ± 4.3	22[c] ± 2.9	62
Juncus balticus	52[c] ± 4.7	39[b] ± 4.3	24
Geum aleppicum	65[a] ± 1.0	24[c] ± 0.5	64

* Data from Hawley *et al.* (1981*a*).
† $N = 10$.
‡ Means within seasons followed by different superscript letters were statistically significantly different ($P < 0.05$) (Student-Newman-Keuls range test).

Table 4
Nutrient digestibility, animal intake, and performance for six bison and six Hereford steers fed sedge hay in summer and winter*

		% digestibility (mean ± SD)						
Season	Species	Organic matter	Energy	Crude protein	Acid detergent fibre	Mean daily intake† ± SD	Average daily gain kg/day	Feed conversion %
Summer	Bison	56.7‡ ± 6.1	51.2‡ ± 3.5	35.8‡ ± 4.3	45.0 ± 5.2	1.6[a§] ± 0.3	0.42[b§]	11.3
	Cattle	48.8 ± 2.7	44.5 ± 2.4	19.6 ± 3.3	40.7 ± 3.1	1.4[a] ± 0.3	0.05[a]	1.2
Winter	Bison	52.8 ± 7.6	50.1 ± 7.7	41.4 ± 11.0	49.4 ± 8.0	1.6[a] ± 0.2‖	0.04[a‖]	0.8‖
	Cattle	49.2 ± 1.5	46.0 ± 1.9	35.7 ± 3.2	44.0 ± 1.9	2.0[b] ± 0.2	0.31[a]	4.0

* Data from Hawley *et al.* (1981*b*).
† Feed dry matter intake as a percentage of body weight.
‡ Species means within seasons were significantly different ($P < 0.05$).
§ Values followed by different superscript letters within columns were significantly different ($P < 0.05$).
‖ $N = 5$.

4.4 Blood experiments

The responses of most blood components to ration CP and DE contents were complex: many blood components that were sensitive to CP and DE levels also varied significantly with animal species and season (Table 6). Five notable components differed significantly ($P < 0.01$) between animal species. The overall mean levels of these components in bison and cattle, respectively, were blood urea nitrogen, 17.1 mg/dL and 14.1 mg/dL; cholesterol, 110 mg/dL and 126 mg/dL; packed cell volume 48 and 35%; hemoglobin 17.8 g/dL and 13.3 g/dL; glutamate oxaloacetate transaminase 97 IU/L and 76 IU/L. The concentration of blood urea nitrogen was positively related to ration CP and negatively related to ration DE (Hawley and Peden 1982). Blood glucose, cholesterol, and alkaline phosphatase were positively related to ration DE.

5. Discussion

5.1. Forage digestion and animal performance

Bison were superior to cattle in the digestion of all forages. That finding agrees with previous observations (Peden *et al.* 1974, Richmond *et al.* 1977) that bison are more able to digest low protein, high fibre forages than cattle, perhaps because of a longer food retention time in bison (Young *et al.* 1977). Differences between bison and cattle in digestibilities in the total fecal collection digestibility trials were not caused by different intake rates because the most significant differences in digestibility occurred during the summer trial when feed intakes were not significantly different.

The ADG and feed conversion rates were greater for bison than for cattle when sedge hay was fed in summer. Rates of intake for bison and cattle did not differ significantly at that time (Table 4). The superior performance of bison can be attributed to their greater ability to digest sedge hay. In the summer trial, the intake rates of digestible CP and TDN by the Hereford steers were below National Research Council recommendations for maintenance of those animals (National Academy of Sciences – National Research Council 1976). However, when the nutrient requirements for gain in cattle were met, as when the high quality ration was fed, Hereford steers exceeded bison steers in ADG even when the greater initial weight of the cattle was taken into consideration. Those results suggested that bison have a production advantage over cattle when feed is of poor quality, which is probably related to the better digestion of the feed by bison. The production advantage is reversed when feed is of adequate quality to meet the nutrient requirements for high performance by cattle.

Any seasonal effect in the fecal collection trials was confounded by the processing of feed. The significant increase in cattle intake from summer to winter can be attributed to the smaller particle size and greater digestibility of the feed in winter (Schneider and Flatt 1975). Increased intake is often associated with a reduction in digestibility (Schneider and Flatt 1975), but the CP content of the feed was slightly higher in the winter trial (Hawley *et al.* 1981*b*), perhaps accounting for the increase in digestibility recorded in that trial.

Several species of wild ruminants have displayed a depressed metabolism and reduced intake in winter (Short 1969, Silver *et al.* 1969, Ozoga and Verme 1970, Kirkpatrick *et al.* 1975, Westra and Hudson 1977), and Christopherson *et al.* (1976) observed that bison calves consumed less than

Table 5
Initial body weight, intake, and performance during the period of maximum growth (March–June inclusive 1976) of six bison and eight Hereford steer calves

Species	Mean initial body weight, kg	± SD	Intake, kg/animal/day	Average daily gain,* kg/day	Feed conversion, %
Bison	202	± 21†	5.5†	0.5†	9.8
Cattle	237	± 14	9.9	1.1	10.9

* Calculated by linear regression.
† Differences between species were statistically significant ($P < 0.05$).

Table 6
Significance of main effects in analyses of variance of eight blood components measured in summer and winter in bison and Hereford steers receiving rations of high or low protein and high or low energy contents

	Effect			
Blood component	Animal species	Protein in ration	Energy in ration	Season
BUN†	***‡	***	***	***
ALP	NS	***	***	NS
Cholesterol	***	***	***	***
GOT	***	**	NS	NS
Glucose	NS	*	***	***
Hgb	***	***	***	***
PCV	***	***	***	***
TSP	***	**	***	NS

† BUN = blood urea nitrogen; ALP = alkaline phosphatase; GOT = glutamate oxaloacetate transaminase; Hgb = hemoglobin; PCV = packed cell volume; TSP = total serum protein.
‡ *($P < 0.05$); ** ($P < 0.01$); ***($P < 0.001$); NS = not significant.

Hereford calves in winter. In the present study, bison displayed the same level of intake in both summer and winter but were able to grow at that level of intake only in summer. That finding suggested that maintenance requirements of bison were greater in winter or that their metabolism was adjusted to limit growth.

Bison did not avail themselves of the improved feed by increasing their intake in the winter trial as did cattle. Indeed, intake was significantly lower ($P < 0.05$) for bison than for cattle in the winter trial (Table 4). Behavioural responses to cold and wind in winter can limit intake in cattle (Bond and Laster 1974, Malechek and Smith 1976). However, the bison did not appear, subjectively, to be limited in this way. In addition, bison hybrids are reported to be more cold tolerant and more capable of winter foraging than are Hereford cattle (Smoliak and Peters 1955). The failure of bison to consume and gain as much as cattle in the winter trial may reflect differences in the adaptive strategies of wild versus domestic species. Beef cattle have been selected for high rates of gain under conditions in which feed quality and quantity are usually not limiting to production. The quantitative and qualitative limitations of food imposed on wild animals in the winter are such that survival, and not growth, are of primary importance. Under such conditions, natural selective pressures would favour maximum digestion of a limited, low-quality food supply. Metabolism could be voluntarily reduced or shifted from growth to maintenance to ensure survival.

In this experiment, cattle performance improved significantly from the summer to the winter trial. That improvement can be attributed to the greater intake and relative digestibility of the feed. The intake rates of digestible CP and TDN during the winter trial were above National Research Council recommendations for maintenance of cattle steers. That concurs with the observation that cattle steers exceed bison steers in rates of gain when rations meet or exceed the standard requirements to obtain weight gains in cattle steers.

Slough sedge and reed grasses are quantitatively the two most important forages in the SRL. Together, they comprise at least 70% of the diet of bison in the area throughout the year (Reynolds *et al.* 1978). Slough sedge had the greatest digestibility of all the plant species tested. When equivalent parts of the plant were compared in equivalent seasons, slough sedge consistently had higher CP and lower CF contents than reed grass. Slough sedge predominates in the diets of bison in the SRL and other areas (Reynolds and Peden, this publication) and would be, quantitatively, an important native forage for cattle introduced to the SRL.

The absence of a significant effect of harvest site on DMD suggested that hay will have similar digestibilities whether harvested from wet or dry meadows. The ratio of sedge to reed grass is approximately 2:1 in wet meadows and 1:60 in dry meadows (Reynolds *et al.* 1978). In view of the different digestibilities of sedge and reed grass, a significant effect of harvest site could be expected. The absence of this effect may have been related to differences in collection times between samples of hay and samples of individual plant species, or to the effects on the net digestibility of hay samples of plant species not tested individually.

Bison would appear to be less sensitive than cattle to the plant species composition of the range because plant species digestibilities were more disparate in cattle than in bison and bison have been shown to display less grazing selectivity than cattle (Rice *et al.* 1974). Some native forages, such as northern reed grass and baltic rush, were poorly digested by cattle and would probably constitute poor forage for cattle. The DMD of summer samples of aleppo avens was high in cattle, but aleppo avens is a minor component of the plant biomass in the SRL (Reynolds *et al.* 1978) and would not, therefore, be a major constitutent of native hay.

The DMDs for winter plant samples were lower in both bison and cattle and the difference in DMD between summer and winter samples was related to the increase in CF content of samples collected in winter. Willow browse is potentially an important winter food because of its high DMD values during that season; however, the winter diet of free-ranging bison contains little willow. The maximum content of willow in bison diets in winter on the SRL was 2% (Reynolds 1976). Therefore, unless range conditions inhibited grazing, willow would not appear to be an important energy source for bison in winter. Winter willow samples also displayed high DMD values in cattle but the potential for using willow twigs as cattle feed in winter requires evaluation.

5.2. Blood composition

The positive correlation between blood urea nitrogen and ration CP and the negative correlation between blood urea nitrogen and ration DE agreed with earlier observations and are related to nitrogen dynamics in the animal (Hawley and Peden 1982). Bison had a greater blood urea nitrogen level than cattle and that was true with a variety of CP and soluble carbohydrate levels in the ration (Hawley and Peden 1982). The recycling of urea to the rumen is proportional, over a wide range of concentrations, to the concentrations of urea in the blood (Houpt 1970). Thus, the results of this study support the suggestion that bison have a greater capacity than cattle to recycle nitrogen (Peden *et al.* 1974), which could result in a more conservative nitrogen balance, thereby permitting bison to survive and be productive on diets of lower nitrogen content. In addition, greater recycling of nitrogen to the rumen could enhance the digestion of poor quality, nitrogen-deficient rations by counteracting the inhibition of rumen fermentation caused by the low availability of nitrogen to rumen microbes.

Blood glucose, cholesterol, and alkaline phosphatase levels were related to energy intake (Hawley and Peden 1982). Differences in blood cholesterol levels between the two species were greatest in winter and may have been related to reduced energy intake by bison in winter and species differences in nutrient partitioning (Hawley and Peden 1982). Relative to cattle, the physiological strategy of bison appears to be one of seasonal and metabolic adaptations to low quality rations in winter and high quality rations in summer.

Forage potential for livestock production

William L. Pringle

1. Abstract

Yield and quality of vegetation from native meadows were studied from 1968 to 1974 on three soil types (Grand Detour, Taltson, and Slave) in the Slave River lowlands (SRL) to assess the potential for beef cattle production. Yield of native vegetation varied significantly among years and sites but averaged between 1500 and 3000 kg/ha, oven-dry weight, in most areas. Quantity of vegetation produced was related to fluctuations in water table. The quality of native grasses was lower than that of sedges, and crude protein levels decreased from 15% in June to approximately 6% in late August.

The most productive domestic forages on unfertilized soils were smooth brome grass (*Bromus inermis* Lyss.), crested wheat grass (*Agropyron cristatum* [L.] Gaertn), reed canary grass (*Phalaris arundinaceae* L.), meadow foxtail (*Alopecurus pratensis* L.), and alfalfa (*Medicago falcata* L.). Forage plant production was most limited by low levels of soil nitrogen. Summer frosts prevented maturation of cereal grains, which could be grown only for green feed or silage.

Because of the many constraints to beef cattle production in the SRL, the potential for a prosperous industry is questionable. Red meat production in the SRL might be enhanced by raising horses.

2. Introduction

The attractiveness of the Slave River lowlands (SRL) for agriculture and livestock ranching stems from the fact that most of the land is open, stone-free, and may be easily plowed and worked. Also, it appears that the meadowlands may be readily and safely grazed by domestic stock. However, questions pertaining to climatic limitations, soil quality, adaptability of introduced plants, and the proper management of native sedges and grasses should be addressed before an agricultural policy for the SRL is prepared.

This study was conducted from 1968 to 1974 in the Grand Detour area of the SRL to assess the potential of the lowlands to produce pasture, native hay, and feed grain in support of commercial production of beef cattle. Productive potential of the SRL was evaluated by measuring the yield and nutritional adequacy of native vegetation, the effect of clipping or grazing on native vegetation, the extent to which introduced plants could improve forage production, and the limitations to crop production by soil nutrients and plant responses to the environment. The results of this research form the basis of the evaluation and assessment of the potential of the SRL for forage and livestock production presented in this report.

3. Methods

3.1. Study sites

Four areas were chosen for intensive study on the basis of important agricultural soil types (Fig. 1). Soil type identification follows Day (1972). Two blocks, each 0.4 ha, were plowed in June 1968, one block on site 1 (a Taltson soil) located in a small meadow of about 120 ha surrounded by willows (*Salix* spp.) and aspen (*Populus tremuloides* Michx.), and the other block on site 2 (a Grand Detour soil) located on the north side of a 60-ha meadow. Those two blocks were summer fallowed in 1968 and seeded in summer 1969. Aspen trees, ranging from 6 to 10 cm in diameter, were cleared from a 0.4-ha block at site 3 (a Slave soil) in November 1968, and the land was broken, root-picked, and summer fallowed in 1969 and seeded in 1970. Site 4 (a wetter Grand Detour soil) was established in 1971 on a large open meadow for use in native vegetation studies. Those study areas will henceforth be referred to by site number.

3.2. Weather

3.2.1. Instrumentation and location — A weather station, with a standard set of Ministry of Transport instruments, was established in June 1968 at site 1 approximately 0.8 km west of the Slave River. There were no trees or shrubs higher than 4 m located within 100 m of the station; however, the site was sheltered on the east and south sides by white spruce (*Picea glauca* [Moench] Voss.). Weather readings were taken at 0800 and 1700 h each day that the operator was present during June, July, and August of each year of the study until 1974. Records of maximum and minimum temperatures, rainfall, total amount of wind (the total kilometres per month), and evaporation from Bellani plates were made. Wind was recorded from Cassela anemometers set 180 cm above the ground and readings were taken once a day. Weather data from site 1 were averaged for the 7-year period (1968–74). Climatological data collected at site 1 were compared with similar records taken at the airports of Fort Smith (56 km south of research site 1 at Grand Detour), Fort Resolution (104 km north), and Hay River (185 km northwest).

A weather station similar to that at site 1 was established in June 1971 at site 4 and was located at least 300 m from shrubs and trees. Weather readings were taken every third day. Recording instruments collected temperatures continuously. Weather data from site 4 were averaged over the 4-year period (1971–74) and were compared with data from site 1 averaged for the same period.

Soil temperatures were taken at depths of 5, 10, 15, 30, and 45 cm at the four experimental sites. Those temperatures were used to determine when the rooting zone became active and when frost had left the ground. Soil temperatures were recorded at least weekly and were averaged by month for each of the study sites.

3.3. Native Vegetation

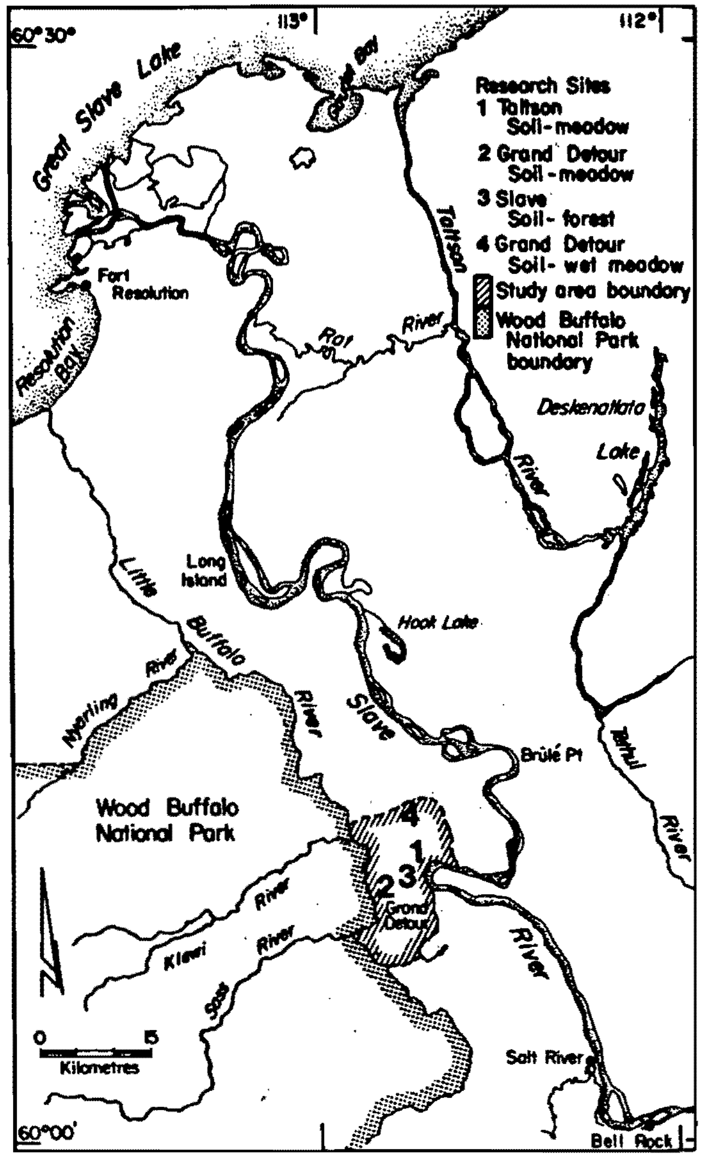
3.3.1 Cutting intensity — Standing native vegetation was harvested at six levels of cutting intensity during June, July, and August from meadows at sites 1 and 2 for each of 3 consecutive years (1968–70) to test the effect of frequency of cutting on yield and persistence of native species. There were six combinations of cutting dates: (1) one cut in June; (2) one cut in June and one in July; (3) one cut in June, one in July, and one in August; (4) one cut in June and one in August; (5) one cut in July; and (6) one cut in August.

A second trial was established at three sites to test the effect on yield of deferring the harvest. The three sites supported three types of native vegetation and were given six harvest treatments during 4 consecutive years (1971–74). The six harvest treatments for each of the 4 years were as follows: 1 = cut (year 1), deferred (year 2), deferred (year 3), cut (year 4); 2 = deferred, cut, deferred, cut; 3 = deferred, deferred, cut, cut; 4 = cut, cut, deferred, cut; 5 = cut, cut, cut, cut; and 6 = cut, deferred, cut, cut. The sites and vegetation types tested were as follows: site 1, a Taltson soil, primarily a stand of beaked sedge (*Carex rostrata*); site 4, a Grand Detour wet soil, primarily a stand of whitetop grass (*Scolochloa festucacea*); and site 2, a Grand Detour soil, primarily a mixture of northern reed grass (*Calamagrostis inexpansa*) and slough sedge (*Carex atherodes*).

3.3.2. Fertilizer trials — Fertilizer trials were established on Taltson and Grand Detour soils at sites 1 and 2, respectively, to test for macronutrient deficiencies and the effect of fertilizer on yield of native vegetation. All plots were cut once each year in late July for 3 years (1968–70). Fertilizer was applied once at the rate of 200 kg/ha each of nitrogen, phosphorus, and potassium; and 40 kg/ha of sulphur. Ammonium nitrate, triple super phosphate, muriate of potash, and flowers of sulphur were the sources of fertilizer elements. The fertilizer trials comprised six treatments: application of nitrogen, phosphorus, potassium, and sulphur; application of nitrogen, phosphorus, and potassium; application of nitrogen and phosphorus; application of nitrogen only; application of phosphorus only; and no application.

Based on the results of the first trial, which indicated that nitrogen was the most limiting nutrient to growth of native vegetation, a rate-of-application trial was established in June 1971 on three areas: (1) a small meadow dominated by water sedge (*Carex aquatilis*) with a low percentage of northern reed grass at site 1, on a Taltson soil; (2) a stand comprising 50% northern reed grass, 20% whitetop grass, and 30% slough sedge at site 2, on a Grand Detour soil; and, (3) a large meadow of primarily whitetop grass at site 4, on a wet Grand Detour soil. Nitrogen fertilizer was applied once in June 1971 at the rates of from 0 to 300 kg/ha in 50 kg/ha increments to test seven treatment applications. A fall fertilization trial was conducted in September 1971 and 1973 where nitrogen fertilizer was applied at the rate of 50 kg/ha to one-half of the macro-plot. Plots were harvested during mid-August for 3 consecutive years (1971–73) on site 1 and for 4 consecutive years on sites 2 and 4.

Figure 1
The Slave River lowlands showing location of agricultural research sites at Grand Detour



3.3.3. Quality — Samples of native hay were cut from five plant associations at the end of June, at the end of July, and at the end of August during 1968–70. The following soil and vegetation types were sampled: (1) Taltson soil, semi-wet, dominated by slough sedge and northern reed grass; (2) Taltson soil, wet, dominated by water sedge; (3) Grand Detour soil, dry, dominated by Canada reed grass (*Calamagrostis canadensis* (Michx.) Beauv.) and slender wheat grass (*Agropyron trachycaulum* (Link.) Malte); (4) Grand Detour soil, semi-wet, dominated by northern reed grass and slough sedge; and (5) Grand Detour soil, wet, dominated by whitetop grass and slough sedge. Vegetation samples were oven dried at 90°C and ground in a Wiley Mill through a 1-mm screen. Samples were then analysed for crude protein (CP), acid detergent fibre (ADF), calcium (Ca), phosphorus (P), potassium (K), magnesium (Mg), zinc (Zn), copper (Cu), and manganese (Mn) contents.

Samples of individual plant species were collected at the end of June, the end of July, and the end of August during 1972–74. Those samples were taken from the same site each time and consisted of entire plants clipped at approximately 2.5 cm above ground or water surface. The following plant species were selected: (1) whitetop, from site 4; (2) water sedge, from the fertilizer plot area on a Taltson soil, site 1 (not taken in 1974); (3) slough sedge, from the east end of site 1; (4) northern reed grass, from a Grand Detour soil type, site 2; (5) fowl blue grass, (*Poa palustris* L.) from a Taltson soil type (site 1), 1972 and 1973 only; (6) American vetch (*Vicia americana* Muhl.), in the forest edge north of site 2, 1973 and 1974 only; and (7) Canada reed grass, north of the site 2 area, 1974 only. Chemical analyses of individual plant species were the same as for the native hay samples except that ADF analyses were not conducted.

Table 1
Weather records for the months of June, July, and August for two sites at Grand Detour on the Slave River

Site	Parameter measured	June	July	August	Total
1 (Taltson soil) Average of 7 years, 1968–74	Total km wind	3866	3681	3581	11 065
	Evaporation, cc	1197	1187	860	3 244
	Air temperatures, °C				
	Mean max.	22.2	23.3	21.7	
	Mean min.	5.0	5.6	5.0	
	Mean	13.9	14.4	13.9	
	Highest	29.4	28.9	29.4	
	Lowest	– 5.01	– 2.2	– 5.0	
	Precipitation, cm	3.51	5.05	5.08	13.69
1 (Taltson soil) Average of 4 years, 1971–74	Total km wind	3969	3705	3353	11 027
	Evaporation, cc	1212	1129	864	3 205
	Air temperatures, °C				
	Mean max.	23.0	23.1	22.6	
	Mean min.	5.5	5.5	4.5	
	Mean	15.0	14.8	14.4	
	Highest	29.6	28.6	30.5	
	Lowest	– 4.2	– 2.5	– 5.5	
	Precipitation, cm	4.60	5.45	4.93	15.06
4 (wet Grand Detour soil) Average of 4 years, 1971–74	Total km wind	4035	4382	3822	12 239
	Evaporation, cc	1195	1250	931	3 376
	Air temperatures, °C				
	Mean max.	22.8	23.9	21.7	
	Mean min.	6.1	5.0	5.0	
	Mean	15.0	15.0	14.4	
	Highest	30.0	30.0	30.0	
	Lowest	– 4.4	– 2.8	– 5.6	
	Precipitation, cm	4.55	5.66	5.46	15.70

3.4. Cultivated forage

Forage adaptation plots were seeded at sites 1 and 2 in 1969, and at site 3 in 1970. Plots consisted of 30 grasses and 11 legumes planted in rows approximately 6 m long and 60 cm apart, with one row for each species. Plots were examined every June to determine amount of winter kill and the current stage of growth. They were examined again in August to record the spreading of plants and the degree of seed set.

3.4.1. Forage variety trials — Ten forage species of proven adaptability under northern conditions, namely brome grass, var. manchar (*Bromus inermis* Lyss.), alfalfa, var. rambler (*Medicago sativa*), intermediate wheat grass, var. chief (*Agropyron intermedium* (Host) Beauv.), crested wheat grass, var. summit (*Agropyron cristatum* (L.) Goertn), timothy, var. climax (*Phleum pratense* L.), alsike clover, var. aurora (*Trifolium hybridum* L.), meadow foxtail, var. common (*Alopecurus pratensis* L.), reed canary grass, var. frontier (*Phalaris arundinaceae* L.), birdsfoot trefoil, var. leo (*Lotus corniculatus* L.), and creeping red fescue, var. boreal (*Festuca rubra* L.) were broadcast seeded on site 2 (a Grand Detour soil) in 1969, seeded in rows spaced 15 cm apart on site 3 (a Slave soil) in June 1970, and seeded in the same manner on site 1 (a Taltson soil) in June 1971. The plots were replicated four times and were cut in mid- to late July of each year for 3 consecutive years. Forage samples, taken from the annual cuttings, were used to calculate dry matter production and chemical contents. The plots were not fertilized.

Four cereal grains, barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), flax (*Linum usitatissimum* L.), and rapeseed (*Brassica campestris* L.), that are normally grown in the Peace River region of north-central Alberta approximately 500 km to the southwest were sown in single four-row plots that were 5 m long and spaced at 21 cm apart. Plots were seeded during the first week of June during 1970–72. Those grains were examined for maturity and seed production and were harvested at the end of August of each year to measure dry matter production. Fertilizer (11-48-0) was applied with the seed at the rate of 100 kg/ha on test plots to determine if it could increase dry matter yield.

3.4.2. Fertilizer trials on brome–alfalfa hay mixture — Nitrogen (N) and P were applied at rates of 100, 200, and 300 kg/ha and K at 100 kg/ha on 1-year-old mixed stands of brome grass, var. carlton (*Bromus inermis*) and rambler alfalfa at the following locations and dates: site 1, June 1971; site 2, June 1969; and site 3, June 1970. All plots were harvested between 15 and 20 July of each year for 3 consecutive years, beginning with the year of fertilizer application. A chopped, 500-g sample from each plot was oven dried at 90°C and used to calculate dry matter production. A subsample was ground through a 1-mm screen and analysed for percentage of N, P, and Ca. The Ca:P ratio and total protein production per hectare were calculated.

3.5. Prediction of animal production

Carrying capacity for cattle was estimated for open or semi-open lands in the SRL. No cost considerations were made for land clearing other than for homestead or brush control along meadow edges. Carrying capacity was calculated using the lowest yields from forage plots from the Grand Detour study sites, using a maximum daily intake rate for livestock, and assuming an 80% calf crop. Nutrient requirements for various classes of livestock were those determined by the National Academy of Sciences – National Research Council (1976).

Linear programming was used to evaluate the economic potential for feeder cattle production in the SRL (Wiens 1977). In that model, income was derived from the sale of feeder calves, feeder yearlings, and culled cows and bulls. Dollar returns were calculated using optimum farm budgets and optimum economic area production estimates for four different levels of cattle prices, two levels of calf crop (72 and 80%), and grazing seasons of different lengths. Gross farm return from cattle was based on the estimated Edmonton price, less the transportation and selling costs. The first set of cattle prices was a 1976 projected price calculated from a 1955–75 regression model in which the Edmonton steer calf price was $1.10/kg and the yearling steer price was $0.82/kg. The three other sets of prices were derived from Edmonton slaughter steer prices: $0.99/kg live weight when feed grain prices were 6.6 cents/kg; $1.10/kg live weight when feed grain prices were 6.6 cents/kg; and $1.21/kg live weight when feed grain prices were 6.6 cents/kg. The steer calf prices for those three price sets were $136, $158, and $183/100 kg, respectively, and yearling steer prices were $106, $121, and $147/100 kg, respectively.

4. Results

4.1. Weather

Killing frosts (– 2.2°C and below) during July were recorded in 4 years (1969, 1971, 1972, and 1974) out of seven at site 1. Temperatures less than – 2.2°C were recorded on 9 days during summer (of which 4 days occurred in July) in 1972. The amount of wind (total kilometres per month) was greater for June than for July or August. The amount of wind varied greatly among years.

Little precipitation fell in June during the driest years of 1969 and 1971 but considerable precipitation fell during June, July, and August in the other years. During 1971–74, the total amount of wind was about 2, 15, and 12% greater in June, July, and August, respectively, at site 4 than at site 1. Site 4 showed a greater rate of evaporation in July and August, similar air temperatures, and a greater average rainfall compared to site 1 during a 4-year period from 1971 to 1974 (Table 1).

Cool soil temperatures prevailed throughout the SRL most of the year (Table 2). A temperature of 5°C was usually reached near the end of May at a depth of 15 cm. Frost was observed in the ground at 60 cm under sod until July 5. Temperature at the 10-cm depth in meadow soil at site 4 reached a high of 12.8°C in 1972 and 1973. At site 1 in a Taltson soil, the maximum temperature at the 10-cm depth was 11.7°C and on the better drained Slave soil at site 3 (forest soil), the maximum was 16.1°C. In 1974, soil temperatures were particularly low in June and were lower at all sites than the 4-year average for that time of year.

Mean daily air temperatures for June during 1968–74 varied less than 2° among all sites. Temperatures at Grand Detour were between those of Fort Smith and Hay River with the least difference in July and August. The monthly maximums for the four locations varied little (Table 3). Mean monthly temperatures at Grand Detour were intermediate to those for the other stations in each of the 3 months. The monthly minimum temperatures for Grand Detour were at least 3°C lower than the next lowest minimum from the other three locations for all 3 months. Greater extremes of temperature were recorded near Grand Detour on the SRL than in the settled areas. Most years, the highest monthly rainfall was in August, at all stations except Fort Resolution (Table 3). Precipitation during the 7-year period (1968–74) was least in 1971 and greatest in 1973 (Northern Research Group 1978).

4.2. Native vegetation

4.2.1. Cutting intensity — Yields of native vegetation varied greatly between years. Annual production, averaged over the six cutting treatments, was 1487 kg/ha oven dry weight (ODW) at site 1 and 1146 kg/ha at site 2 for the 3-year period 1968–70 (Northern Research Group 1978). The plots on site 2, a drier site, had greater variation in yield than those on site 1. A single cut in June provided the least vegetation of all cutting treatments. Single cuts in July and August produced the greatest yields. Yields from the August cut were usually greater than the yields from the July cut, but the differences were not statistically significant. Forb cover increased, sedge cover decreased, and grass cover increased as the number of mowings increased.

In the deferred hay trial, yields were greatest at site 1 (a beaked sedge plant community), followed by site 4 (primarily whitetop grass), and then by site 2 (a mixture of northern reed grass and slough sedge) (Table 4). Site 1 was flooded in 1974 so the plots were not cut. The greatest reduction in annual herbage yield resulted from continuous cutting on the drier Grand Detour soil at site 2 over the 4-year trial. Continuous cutting over the 3-year trial on the wet Taltson soil at site 1 resulted in a negligible reduction. Total cumulative herbage yield summed over the 4 years was greatest for those plots that were cut every year (Table 4). Few seed heads of northern reed grass were observed in plots at site 2 that were cut the previous year when compared to plots on the same site that had not been previously cut.

Table 2
Monthly mean soil temperatures (°C) for June, July, and August for four sites in the Grand Detour area (average of 4 years 1971–74)

Site	Month	Soil depth, cm 5	10	15	30	45	60	90
1 (Taltson soil)	June	8.3*	8.3	7.2	5.6	2.2	0.6	0
	July	10.0	10.0	9.4	7.8	5.0	3.3	0.6
	August	8.9	9.4	8.9	7.8	5.6	4.4	2.8
2 (dry Grand Detour soil)	June	7.2	6.7	6.2	5.1	2.9	2.2	0.6
	July	11.3	10.0	9.5	8.9	7.2	6.1	3.3
	August	18.2	10.7	10.7	10.2	10.1	8.9	6.7
3 (Slave soil)	June	10.7	9.8	9.7	8.2	6.5		
	July	13.3	12.7	12.9	10.7	10.9		
	August	12.9	12.5	12.1	12.1	11.1		
4 (wet Grand Detour soil)	June	7.3	6.8	6.2	4.7	2.6		
	July	10.4	10.0	10.0	8.9	7.2		
	August	10.4	11.0	10.5	9.4	8.9		

* Readings were taken in the morning.

Table 3
Comparison of air temperatures (°C) and total monthly precipitation (cm) for three settled locations in the Northwest Territories and for the Grand Detour area

Parameter*	Location	June	July	August
Mean monthly temperature, °C	Fort Smith	14.4	15.6	13.9
	Fort Resolution	12.8	15.0	13.3
	Hay River	12.8	15.6	13.9
	Grand Detour	13.3	14.4	13.3
Monthly maximum temperature, °C	Fort Smith	29.4	28.9	30.0
	Fort Resolution	27.2	27.2	27.8
	Hay River	28.9	29.4	30.6
	Grand Detour	29.4	28.9	29.4
Monthly minimum temperature, °C	Fort Smith	– 0.6	2.2	– 1.1
	Fort Resolution	– 1.7	1.1	– 1.1
	Hay River	1.1	5.0	2.2
	Grand Detour	– 6.0	– 2.2	– 5.0
Precipitation, cm	Fort Smith	4.29	5.44	5.49
	Fort Resolution	2.46	4.75	4.32
	Hay River	2.67	3.73	4.57
	Grand Detour	3.50	5.05	5.10

* Seven-year average (1968–74) for June, July, and August.

Table 4
Seasonal herbage yields (kg/ha, oven dry weight) of native vegetation as affected by deferred haying from three meadow areas at Grand Detour

Site	Harvest treatment	Year 1	2	3	4	Current annual growth, kg/ha — Harvest years 1971	1972	1973	1974	Total
1 (Taltson soil, wet) Dominant plant = *Carex rostrata*	1 =	C*	D	D		5296			not cut	5296^{c†}
	2 =	D	C	D			3374		not cut	3374^{d}
	3 =	D	D	C				5584	not cut	5584^{c}
	4 =	C	C	D		6153	4112		not cut	10265^{b}
	5 =	C	C	C		5586	4018	4946	not cut	14550^{a}
	6 =	C	D	C		5842		4699	not cut	10541^{b}
4 (Grand Detour soil, wet) Dominant plant = *Scolochloa festucaceae*	1 =	C	D	D	C	3800			3573^{a}	7373^{c}
	2 =	D	C	D	C		1673		3489^{a}	5162^{d}
	3 =	D	D	C	C			2879	2779^{b}	5658^{d}
	4 =	C	C	D	C	4055	2014		3166^{ab}	9235^{ab}
	5 =	C	C	C	C	3205	1787	2056	2921^{ab}	9969^{a}
	6 =	C	D	C	C	3262		2618	2892^{ab}	8772^{b}
2 (Grand Detour soil, semi-wet) Dominant plants = *Calamagrostis inexpansa* and *Carex atherodes*	1 =	C	D	D	C	3969			3573^{a}	7542^{b}
	2 =	D	C	D	C		1248		3204^{ab}	4452^{c}
	3 =	D	D	C	C			2503	2269^{bc}	4772^{c}
	4 =	C	C	D	C	3969	1418		3431^{a}	8818^{ab}
	5 =	C	C	C	C	4820	1361	1939	1844^{c}	9964^{a}
	6 =	C	D	C	C	4376		2770	2212^{bc}	9358^{ab}

* C = cut, D = deferred.
† Totals followed by the same letter are not significantly different ($P > 0.05$).

4.2.2. Fertilizer trials — Native vegetation production showed a significant and positive response to N fertilizer until the third year. There were no significant effects on yield by addition of P, sulphur (S), or K. Annual yield on the Grand Detour soil at site 2 varied more than that on the Taltson soil at site 1. Yields on both areas were 1.5 – 3 times lower during the dry year of 1969. Forage uptake of P increased by approximately 30% in areas where that element was applied (Northern Research Group 1978).

Greater vegetation yields were also observed on all three sites with the application of N fertilizer in the varying rate trial. Maximum annual yields were achieved during the first year after application at an application rate of 100 kg of N/ha on site 1, 250 kg/ha on site 2, and 150 kg/ha on site 4. Plots on site 1 were flooded in 1974 and could not be harvested.

Vegetation yield totalled over all years was maximized at fertilization rates of 300 kg of N/ha/year at sites 1 and 4, and 250 kg of N/ha/year at site 2 (Table 5). Maximum annual vegetation yields at site 1 for the second and third year after application of N fertilizer were achieved by the rates of 200 and 300 kg/ha, respectively. At site 2, the maximum annual yields for the second and third year after application were achieved at the 250 and 300 kg/ha rates, respectively, and in the fourth year, the maximum yield was recorded for the 150 kg/ha rate (Table 5). Significant annual increases ($P < 0.05$) in vegetation yields occurred each year for up to 3 years after application at sites 1 and 2 using the 200 kg/ha or higher application rate, when compared with the 0 rate. However, a significant increase in vegetation production was not obtained at site 2 in the fourth year of harvest after application at any rate of N fertilization. At site 4, all rates of fertilization resulted in higher annual vegetation yields for each of the 4 harvest years (Table 5). The fall application of N fertilizer at the rate of 50 kg/ha caused significant increases ($P < 0.05$) in herbage production the following year on all sites. Total vegetation yield was not significantly affected by the use of S on three sites. On a total yield basis, site 1, the sedge community, yielded nearly as much in 3 years as sites 2 and 4 produced in 4 years.

The CP content of native vegetation was 11.8% averaged for all fertilizer treatments for vegetation cut in 1971 on site 1, 10% for site 2, and 7% for site 4 (Northern Research Group 1978). The native vegetation harvested from

Table 5
Annual production of native vegetation harvested in mid-August in each of 4 years (1971–74) from plots receiving varying rates of nitrogen fertilizer at Grand Detour

Site	Application,* N fertilizer, kg/ha	Vegetation production, kg/ha — Year of harvest (mid-August) 1971	1972	1973	1974	Total
1 (Taltson soil)	0	3176^{b†}	3190^{d}	2992^{b}	—	9 358^{d}
	50	4082^{d}	3630^{c}	3286^{b}	—	10 998^{bc}
	100	4519^{a}	3728^{c}	2911^{b}	—	11 158^{b}
	150	3971^{e}	3787^{bc}	3317^{b}	—	11 073^{b}
	200	3856^{f}	4297^{a}	4186^{a}	—	12 338^{a}
	250	4252^{c}	4041^{ab}	3994^{a}	—	12 287^{a}
	300	4395^{b}	4240^{a}	4219^{a}	—	12 855^{a}
2 (Grand Detour soil)	0	3487^{b}	1446^{d}	2174^{f}	2056^{a}	9 163^{c}
	50	4055^{g}	1730^{cd}	2458de	2353^{a}	10 597^{bc}
	100	4366^{f}	1772^{bcd}	2414^{e}	2410^{a}	10 962^{b}
	150	4817^{b}	2112^{b}	2587^{cd}	2510^{a}	12 027^{ab}
	200	4764^{c}	2056^{bc}	2686^{c}	2197^{a}	11 703^{ab}
	250	5191^{a}	2467^{a}	3000^{b}	2325^{a}	12 983^{a}
	300	4735^{d}	2070^{bc}	3502^{a}	2212^{a}	12 519^{a}
4 (wet Grand Detour soil)	0	3033^{b}	2240^{d}	2389de	3318^{cd}	10 981^{d}
	50	3699^{c}	2694^{bc}	2864^{c}	3302^{d}	12 560^{c}
	100	3176^{g}	2438^{cd}	2379^{e}	3203^{b}	11 198^{d}
	150	3947^{a}	2879^{b}	3045^{b}	3999^{b}	13 868^{b}
	200	3772^{b}	2666^{bc}	2462de	3601^{bcd}	12 500^{c}
	250	3431^{f}	2836^{b}	2856^{c}	3715^{bc}	12 838^{c}
	300	3630^{d}	3573^{a}	3522^{a}	4253^{a}	14 978^{a}

* Fertilizer was applied only once in June 1971.
† Within columns, means followed by the same letter are not significantly different ($P > 0.05$).

sites 1 and 2 showed increased levels of CP content associated with increased rates of N fertilization. Those higher levels were maintained until the end of the second year and vegetation from site 4 maintained that increase until the end of the third year. A fall application of N fertilizer at the rate of 50 kg/ha produced significant increases in CP contents of native hay for the harvest year immediately following the year of application on all sites.

4.2.3. Quality — Native vegetation hay samples showed a marked decrease in CP with advance of season, but this decrease was less pronounced for wet meadows than for dry (Table 6). Sedge hay and hay comprising a mixture of sedge and grass had higher CP levels in all seasons than did hay composed primarily of grasses. Vegetation CP levels were higher in 1969 than in 1968 or 1970. Acid detergent fibre levels increased with advance of season and the degree of change paralleled the decrease in CP levels (Table 6). Phosphorus levels in the vegetation declined from June to August on all sites, most markedly between June and July on wet sites and between July and August on a dry site (Table 6). The pattern of Ca content was the reverse of that of P, increasing with advance of season. The Ca:P ratio was lowest in June at all sites, increased as the season progressed, and exceeded 6:1 in one sample from the wet Grand Detour soil in August. The K level in vegetation from site 1 was high, particularly in early cut forage. Zinc content in vegetation samples did not change appreciably with maturity of the vegetation but levels were generally lower in samples from Grand Detour soils compared to those from Taltson soils. Manganese content was higher in vegetation from wet sites than in that from drier sites regardless of soil type (Table 6). Levels of Cu were higher in vegetation samples from Taltson soils than from Grand Detour soils and were higher in samples from wet meadows than a dry meadow (Table 6). Copper content in the vegetation decreased substantially with advance of season.

Table 6
Average values for chemical composition of current season's growth of native hay samples from specific sites at Grand Detour, 1968–70

Site	Vegetation type	Date cut (end of)	Percent: Crude protein	Acid detergent fibre	Mg	K	Ca	P	Ca:P	ppm: Zn	Mn	Cu
1 (Taltson soil, semi-wet)	*Carex atherodes*	June	15.3	27.3	.13	2.8	.32	.30	1.1	57	148	9.7
	and	July	12.5	28.8	.13	2.2	.44	.16	2.7	53	107	7.2
	Calamagrostis inexpansa	August	10.8	32.1	.13	1.8	.61	.15	4.2	66	144	4.7
1 (Taltson soil, wet)	*Carex aquatilis*	June	14.2	28.2	.13	2.4	.36	.22	1.6	33	234	10.7
		July	11.4	29.1	.12	1.9	.48	.17	2.8	33	252	7.9
		August	10.0	31.7	.12	1.5	.65	.14	4.6	32	351	3.9
2 (Grand Detour soil, dry)	*Calamagrostis canadensis*	June	10.0	34.9	.13	1.2	.31	.21	1.5	29	101	2.5
	and	July	8.7	35.5	.13	1.0	.36	.20	1.8	24	127	2.0
	Agropyron trachycaulum	August	6.5	38.4	.12	0.6	.41	.14	3.0	22	113	1.9
2 (Grand Detour soil, semi-wet)	*Calamagrostis inexpansa*	June	12.2	32.0	.14	1.7	.31	.21	1.5	29	156	3.8
	and	July	9.4	36.0	.14	1.2	.38	.16	2.3	25	160	1.9
	Carex atherodes	August	7.7	37.4	.15	0.8	.52	.11	4.7	30	184	1.7
4 (Grand Detour soil, wet)	*Scolochloa festucacea*	June	11.6	29.1	.11	1.9	.44	.16	2.8	41	241	6.4
	and	July	10.0	32.3	.11	1.6	.52	.12	4.3	39	207	4.1
	Carex atherodes	August	8.6	34.2	.11	1.0	.65	.10	6.8	38	250	2.1

Table 7
Average values for chemical composition of forage species at Grand Detour, 1972–74

Plant species	Month	Percent: Crude protein	Mg	K	Ca	P	Ca:P	ppm: Zn	Mn	Cu
Scolochloa festucacea (3 years) (grass)	June	10.3	.11	1.8	.23	.14	1.7	29	91	4.5
	July	8.9	.09	0.9	.19	.06	3.0	19	56	1.2
	August	6.1	.14	0.6	.34	.06	4.3	28	114	1.1
Carex aquatilis (2 years) (sedge)	June	13.1	.14	2.6	.37	.19	2.0	76	194	10.6
	July	10.8	.13	2.3	.40	.17	2.4	84	241	7.6
	August	7.2	.13	1.8	.54	.13	4.2	70	227	3.0
Carex atherodes (3 years) (sedge)	June	14.4	.13	2.2	.37	.21	1.8	74	101	11.5
	July	10.6	.12	2.2	.41	.13	3.2	83	114	7.1
	August	8.9	.13	2.1	.49	.01	4.9	98	127	5.3
Calamagrostis inexpansa (3 years) (grass)	June	11.3	.11	1.3	.24	.19	1.2	16	133	1.8
	July	9.0	.10	1.2	.30	.15	1.9	17	142	1.7
	August	7.4	.11	0.8	.38	.15	2.6	15	157	1.2
Poa palustris (2 years) (grass)	June	7.8	.10	1.7	.19	.20	0.9	46	50	2.8
	July	7.2	.08	1.0	.17	.13	1.3	34	56	1.5
	August	5.6	.07	0.6	.18	.08	2.4	31	58	0.9
Vicia americana (2 years) (forb)	June	24.5	.25	2.4	.76	.30	2.6	60	58	4.9
	July	20.4	.24	2.3	1.04	.31	3.3	57	32	8.5
	August	17.6	.28	1.6	1.22	.22	5.6	34	16	7.9
Calamagrostis canadensis (1 year) (grass)	June	9.4	.08	1.1	.35	.14	2.6	50	174	3.1
	July	8.6	.08	0.9	.38	.13	3.0	48	241	1.4

Results of chemical analyses of individual plant species were similar to those for the native hay samples regarding level of nutrients and changes with advanced phenology (Table 7). Crude protein levels were highest in June for both sedges and grasses. However, sedges were usually higher than grasses in CP contents in each season. American vetch, a forb, contained the highest levels of CP and P throughout the summer.

4.3. Cultivated forage

The perennial species that were seeded in forage adaptation plots and showed good initial growth and high yields for 4 years post-seeding were climax timothy, chief intermediate wheat grass, revenue slender wheat grass, boreal creeping red fescue, aurora alsike clover, and leo birdsfoot trefoil. Those species that showed high yields and persistence for 8 years post-seeding were fairway crested wheat grass, meadow foxtail, reed canary grass, Russian wild rye (*Elymus junceus* Fisch.), smooth brome grass, and falcata alfalfa (*Medicago falcata* L.). Meadow foxtail had spread by seed dispersal and occurred over most of the plot area by 1975.

4.3.1. Forage variety trials — Site 2 plots on a Grand Detour soil produced high first year yields of forage. By the second year, the alfalfa had diminished and little trefoil remained. Some of the grasses appeared to be suppressed and yields were reduced. Plots were destroyed by fire during the third year but the alfalfa plots recovered and yielded in excess of 4000 kg/ha by the fourth year. Only alfalfa, brome grass, intermediate wheat grass, and meadow foxtail plots were worth cutting in that year.

The Slave soil plots (site 3) showed poor establishment because of crusting and baking of the soil surface. Once established, alfalfa had the highest yield followed by intermediate wheat grass and brome grass. Vegetation yields on that site were lower than on sites 1 or 2.

The Taltson soil plot (site 1) produced high yields during the first harvest year. Creeping red fescue, intermediate wheat and crested wheat-grasses produced in excess of 4000 kg/ha dry matter. Vegetation yields in the second year exceeded 2000 kg/ha with intermediate wheat grass, brome grass, and crested wheat grass having the highest production. Alfalfa, crested wheat grass, timothy, and meadow foxtail all yielded more than 3000 kg/ha in the third year.

Forage produced on Taltson soil was higher in CP content than that from the other two locations. Legumes were higher in CP than grasses.

Total dry matter production from single harvests per year ranged from 1000 to 4700 kg/ha for the three sites. A good second growth of vegetation had occurred by the end of August on all plots that had been previously cut, particularly the legumes. Considerable rainfall followed the first harvest in 1970 and again in 1973. In those years, the dry matter production of second growth vegetation on plots at site 1 was estimated to be in excess of 800 kg/ha.

Summer frosts prevented any cereal grains from maturing. Plots were cut for green feed at the end of August. Barley and oat yields averaged 3781 kg/ha ODW and 4576 kg/ha ODW, respectively. Use of 100 kg/ha of 11-48-0 fertilizer applied with the seed resulted in a 33% increase in dry matter yield for barley and wheat and a 16% increase for oats and flax. The largest increases occurred at sites 1 and 2 on the two meadow soils.

4.3.2. Fertilizer trials on brome–alfalfa hay mixture — Fertilized plots yielded 4922 kg/ha ODW on the Taltson soil (site 1), 3418 kg/ha on the Grand Detour soil (site 2), and 2691 kg/ha on the Slave soil (site 3). The grass–legume forage on site 1 was not responsive to additional N but increasing application of P increased P content in the forage. The CP level of the forage averaged less than 10% and was not affected by the fertilizer treatments over 3 harvest years. The yield and persistence of alfalfa was not changed by the fertilizer treatment at site 1. The Ca:P ratio was 8:1 for forage samples taken where no P was applied, whereas the overall plot average was about 7:1.

Greater annual variation in forage production and lower total yields were noted in plots from site 2. Herbage yield of the grass–legume mixed forage for 3 years averaged 2793 kg/ha without additional N but was 3241 kg/ha and 3672 kg/ha per year for application rates of 100 and 200 kg/ha of N, respectively. Those forage yield increases were not large and the magnitude of increase tended to decline with time. The P content of the forage was low in all years, averaging less than 0.14%. Applications of P tended to cause increases in the P content of the forage but an optimal level of 0.2% was never reached. Calcium levels in forage samples averaged 0.5%. A second growth of forage was estimated to yield about 400 kg/ha in late August. At the end of 4 years, the alfalfa in the plots had died out leaving a dominant stand of brome grass.

Increases in dry matter were not significant after the second harvest year on site 3. Dry matter production on that soil type was the lowest of the three types tested. The CP content of forage from that site averaged 11% compared to an average of 8.7% for the meadow soil areas. The P content of forage samples averaged 0.2%, a level that was increased with the addition of P at the rate of 300 kg/ha. Regrowth in late August was estimated to be approximately 400 kg/ha.

4.4. Prediction of animal production

Total cultivated hay production potential for the SRL was about 411 795 t based on an average vegetation yield of 2.5 t/ha (tonnes, 1 t = 1000 kg) and 55% arability on the Grand Detour soils (sites 2 and 4) and 4.0 t/ha and 33% arability on the Taltson soils (site 1). Production of native meadow hay from selected meadows was estimated to be 22 115 t based on yields of 1.5 t/ha and 3.0 t/ha for 10% and 20% availability on the Grand Detour and Taltson soils, respectively. Thus, total forage available for winter feed approximated 433 910 t. A cow–calf unit requires 11.6 kg of hay per day, and a cow–yearling unit 16.9 kg of hay per day for winter maintenance (National Academy of Sciences – National Research Council 1976). Stored forage would be required for approximately 230 days or 2.7 t of forage per animal unit per season for a cow–calf operation and 3.9 t of forage per animal unit for a cow–yearling operation. The carrying capacity of the land would then approximate 110 000–160 000 cows, depending upon the type of livestock operation. Cattle could be stocked at a rate of 13–19 cows/km^2. For cow–calf and cow–yearling systems, production of live animals would be 32 945 t and 37 271 t per year, respectively.

When the steer calf price was $1.10/kg live weight with an 80% calf crop (price projected from regression model) there was a return of $8 per cow per season. When the steer calf price was $1.83/kg with an 80% calf crop the return was $121 per cow per season. At that level, which approached 1978 October prices for calves ($2.20/kg), the returns from a 100-cow herd would approximate $12 000.

5. Discussion

5.1. Weather

Temperatures below killing frost (– 2.2°C) were recorded during July in most years. Such frosts are detrimental to seed set in grasses and prevented kernel formation in cereal crops. Production of crops other than for green feed or hay would be a decided risk. High winds and low precipitation contributed to a large amount of evaporation; evaporation rate was greatest in June when winds were greatest, rainfall was the least, and temperatures were the lowest of the summer months (June to August). The amount of precipitation varied greatly both monthly and annually and during summer was the most important factor affecting yield of native vegetation; yields were lowest in years with the least summer precipitation.

Hay River recorded the lowest mean June daily temperatures and the highest mean July and August daily temperatures of the four locations. That temperature pattern suggested the influence of lake ice during the early part of the summer. A similar situation was expected for Fort Resolution but mean temperatures for July and August were lower there than at the other locations. Perhaps air moving eastwards from the mountains and over the northern Slave River caused cooler temperatures at Fort Resolution.

Fort Smith and Grand Detour received more rain during June, July, and August than the two stations located on Great Slave Lake at Fort Resolution and Hay River. Weather records show great variability among years and among months in any one year.

The lower than normal soil temperatures in 1974 are difficult to explain because air temperatures for that year were average. However, perhaps they resulted from the lower than average air temperatures at Fort Smith and Fort Resolution in November 1973, which could have caused a greater depth of frost during winter 1973–74 and lower soil temperatures the following summer.

5.2. Native vegetation

5.2.1. Cutting intensity — The low vegetation yield from the June cut in most years would make this an impractical time for harvesting native hay. Cutting once in mid-July offered the most efficient system of preparing native hay. Because native vegetation requires at least 40 days to recover from an initial cutting, in general, native meadows should be harvested only once yearly for hay.

Native vegetation showed large annual variations in yield. That would have serious implications for commercial operators using the area for range or for growing winter feed. In terms of total amount of vegetation produced, consecutive annual harvests would be the most productive technique for haying native meadows. However, on a drier area (site 2), annual yields were lower as a result of consecutive cutting. Therefore, annual production on drier sites could be increased by cutting in alternate years rather than every year. Variation in vegetation production appeared to be directly related to July temperatures and precipitation.

Northern reed grass produced more seed heads when cut in alternate years than when cut annually. Carbohydrate reserves in the roots may have been greater in plants cut biannually, resulting in greater seed head production in alternate years. Little regrowth of this forage occurred after cutting; therefore, there was little green growth available to replenish root reserves before freeze-up. That type of plant community would probably deteriorate in quantity and quality if cut annually.

5.2.2. Fertilizer trials — Nitrogen was the most limiting macronutrient to growth of native vegetation in the SRL and can be used to increase production. Applications of P and S had a negligible effect on vegetation production; applications of P at the rate of 200 kg/ha resulted in a 30% increased uptake of this element in native vegetation. Therefore, levels of P can be improved in the vegetation of native meadows by broadcast applications of this element to the soil.

Although total vegetation yields (summed for 3 or 4 years) were greatest at fertilization rates of 300 kg of N/ha at sites 1 and 4 and 250 kg/ha at site 2, the magnitude of the increase in annual yield within each year over the lowest rate of fertilization (50 kg/ha) was not great. In addition, the fall application trial of 50 kg of N/ha resulted in a significant increase in vegetation production the following harvest year on all sites. Small yearly applications of N (50 kg/ha) would appear to be as effective as large single treatments that tend to lose their positive effect after two or three harvest seasons. The greatest response to N fertilization, as reflected by a 42% increase in vegetation production, was obtained on site 2 plots (the grass–sedge mixture). Site 1 (the sedge stand) and site 4 (the grass stand) responded with maximum increased yields of 37 and 36%, respectively. All three vegetation types exhibited positive responses to N fertilizer. Site 4 plots continued to respond with the highest annual yields being attained at the highest rate of fertilizer application (300 kg/ha). Additional increases in vegetation yield might be obtained with increased fertilizer application. Site 1, the water sedge stand, produced the greatest quantity of vegetation of the three sites studied, indicating the importance of this vegetation community to the production potential for the region.

Sedge plants from site 1 had the highest levels of CP whereas grass from site 4 had the lowest, suggesting that native sedge communities contain higher CP contents than do grass communities and would be better pasture areas. Nitrogen applications were more useful on sedge or sedge–grass mixed plant communities than on strictly grass communities because of a greater response to added N by sedge plants as reflected in the higher CP content of sedge hay. This probably occurred because soil moisture was not limiting to the sedge stands.

5.2.3. Quality — If native vegetation is cut for hay during late July or early August, CP content would vary between adequate and marginal, Cu content would be marginal, P content would be inadequate, and other nutrients would be adequate to meet maintenance levels for most classes of beef cattle (National Academy of Sciences – National Research Council 1976). Hay cut in late August would be generally inadequate in quality to provide a maintenance diet for livestock. Native hay should be prepared at the end of June, if the objective is to provide hay of adequate quality to maintain beef cattle. The higher protein level recorded for hay harvested in 1969 compared to that in 1968 and 1970 could possibly reflect the cool dry season in 1969. Hay samples from Taltson soils tended to be higher in P content than those from Grand Detour soils, indicating that Taltson soils may be more effective at mobilizing P.

The P level in a ration should be at least 0.18% for growing beef cattle (National Academy of Sciences – National Research Council 1976). Of the seven plant species analysed, all except American vetch would be limiting in P content by the end of July (Table 7). Calcium requirements are equivalent to those of P, and the Ca:P ratio should not exceed 6:1 (National Academy of Sciences – National Research Council 1976). All hay and individual plant species collected in June, July, and August contained adequate supplies of Ca for proper maintenance of beef cattle except the fowl blue grass sample in July. Whitetop grass and northern reed grass appeared to be inadequate for Zn content.

In the Hook Lake area of the SRL, bison usually grazed only the top third of plants in wet meadows (Reynolds *et al.* 1978) which would result in consumption of a diet higher in CP. However, if native vegetation was to be the main source of forage for livestock, it would be necessary to supply P, supplemental protein, and mineralized salt containing Cu and Zn.

5.3. Cultivated forage

5.3.1. Forage variety and cereal grain trials — Alfalfa and brome grass were the least variable in yield and contained the highest level of CP of the forage species tested on the three soil types. Therefore, these species would be the best for production of cultivated hay. Meadow foxtail, crested wheat grass, and creeping red fescue would be the best adapted cultivated forages for grazing purposes. However, grass species would require annual applications of N for sustained production. Meadow foxtail and reed canary grass spread throughout the plots more than the other species, indicating that they can become established despite severe competition. Moisture was the main limiting factor to production of forage crops on the Slave soil type.

Production of annual cereal grain crops was limited by a low level of precipitation in June. Seeding earlier would have little advantage because soils would be cold and germination would not likely occur until after the first of June. Existing varieties of grain could not mature in the SRL because the season is usually too short as a result of killing frost. Thus, in the SRL cereal crops could be grown only for green feed or silage.

5.3.2. Fertilizer trials on brome–alfalfa hay mixture — The Taltson soil type (site 1) had good growing potential with apparent high fertility that was not affected appreciably by heavy applications of fertilizers. The Ca:P ratio (8:1) was high in forages grown on the Taltson soil; hay produced on this soil type would require P supplementation if it were to be fed to beef cattle. The Grand Detour soil type (site 2) appeared to be deficient in N because increased yield of the brome–alfalfa mixture occurred annually over 4 years with only one application of N at the rate of 200 kg/ha. The forested Slave soil (site 3) was generally dry, which seriously hampered production of the grass–legume mixture. Addition of N to this soil type resulted in greater vegetation production over 2 harvest years and the addition of P had little or no effect.

Good stands of grass–legume mixture were established on all three sites. Applications of N and P increased vegetation yield but those increases were small in comparison to the rates of fertilizer applied. The Grand Detour soil was the most responsive to fertilizer treatment and the Taltson soil was the least responsive. However, the Taltson soil was the most productive in terms of total quantity of the grass–legume hay mixture produced. Alfalfa had diminished by the end of the fourth year on all sites and vegetation stands within the plots were dominated by brome grass. The application of fertilizer did not appear to affect this change in plant species composition. Brome grass was more aggressive and dominated alfalfa, regardless of the nutrient content of the soil.

5.4. Productive potential

Forested areas will support some grazing in the SRL, but summer feed for livestock must come primarily from the numerous meadows scattered throughout the region. Up to 10% of the meadow areas may be saline to an extent that would adversely affect crop production (Pringle *et al.* 1975). Plot yields are generally higher than yields on a field scale. Therefore, the lowest values of vegetation yields obtained during this study were used to provide conservative estimates of total vegetation production. Also, a maximum daily allowance of feed for each class of livestock, in addition to an 80% calf-crop estimate, was used in calculating carrying capacity for cattle.

The economic return from a 100-cow herd was approximately $12 000, based on October 1978 prices. That was considered to be the minimum required to cover basic living costs and refinancing of a beef cattle operation. Because inflation and increased production costs have more than kept pace with the rising slaughter price for beef, beef cattle enterprises in the SRL could only be viable if they were large (100–200 cows), well capitalized, and well managed and if cattle prices were maintained at a high level in comparison to production costs.

The many constraints to beef cattle production in the SRL include the presence of bison infected with brucellosis and tuberculosis, the presence of anthrax (Broughton, this publication), the long winter feed period of up to 7 months, the prevalence of pest insects at high densities, the presence of predators (Van Camp, this publication) that have a haven in Wood Buffalo National Park, the low quality of native vegetation, the potential soil salinity problems for crop production, and the tendency of flooding for much of the land. Therefore, the potential for a prosperous cattle industry in the SRL is questionable.

5.5. Prospects for free-ranging horse production

Cattle can range free for only about 4–5 months of each year in most areas of northern Canada without supplemental feed. Early frosts hamper grain production, and the quality of available native forage is barely suitable for the maintenance of cattle. Horses may be more suitable for meat production in the SRL because they appear to cope better with insect pests and can survive on lower quality feed better than cattle when quantity is not limiting, as is the case in the SRL. Horses have a greater capacity to forage through snow than do cattle (Andreyev 1971), and feral horses are capable of surviving in a variety of habitats (Cook 1975). However, survival problems could arise when snow depths exceed 50 cm or when crusting occurs. Horses are well adapted to severe winter conditions in Yakutskaya in Siberia, where most adult animals remain on pastures throughout the year (Andreyev 1971). In the USSR, foals gained 1–1.2 kg/day prior to weaning and their survival rate was as high as 97% in herds consisting of 65% mares and one stallion for every 11 mares.

Three horses survived in the SRL near the Taltson River from 1958 to 1976. They were thought to be remnants of a group of 30 horses released in 1958 by a local outfitter. However, horses are susceptible to some of the diseases of bison, and inoculations against anthrax would be required if horse production were to be undertaken in the SRL. Also, equine infectious anemia (swamp fever) could pose a major problem for prospective horse ranching because of a lack of treatment for that disease. The requirement to maintain infected horses in fly-proof isolation could be economically impractical for a viable commercial operation.

Horses are in demand for work stock, bucking horses, and meat, and the demand for meat is increasing. In spring 1978, horse meat buyers in Grande Prairie, Alberta, paid an average of $1/kg live weight, and competition for horse meat at that time forced a price increase. Alsask Processors, Edmonton, killed about 90 animals a day during 1977 and there was little change in the quantity of horses processed in that plant over the next 4 years (Mr. Bernardi, pers. commun.). Ninety percent of the horse meat processed in Edmonton in 1977 was exported to Japan and Europe (J. Ratcliff, pers. commun.). Horse ranching should be considered in any land-use evaluation of the SRL because horses appear to be suitable for meat production in an economically viable operation.

Management alternatives for ungulate production in the Slave River lowlands

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1. Factors affecting bison production

The bison population in the Slave River lowlands (SRL) increased from an estimated 350 animals in 1948 to more than 2000 animals by 1971. That population decreased to about 300 animals during the next 14 years, with the most precipitous decline occurring after 1974 (Reynolds and Hawley, *Introduction*, this publication; Van Camp and Calef, this publication). Productivity in the Hook Lake population was the lowest recorded in the literature for bison in North America (Van Camp and Calef, this publication). The low rates of reproduction, calf survival, and recruitment to the yearling age class of the SRL bison herd are primarily attributable to a combination of hunting, predation by wolves, and disease. The individual effects of these mortality factors were confounded and it was not possible to determine their relative importance to the SRL population. The growth rate (r_i = 0.233) of a population of wood bison in the Mackenzie Bison Sanctuary (MBS) was considered to be near the maximum rate of increase possible for bison under natural conditions in northern environments (Calef 1984). Protection from hunting, little or no predation by wolves, and an apparent lack of disease in the MBS are believed to be the major reasons why that bison population has continued to grow at an exponential rate (Government of the NWT 1983).

Hunter kills equalled or exceeded the total annual recruitment of bison during all years of study (Van Camp, this publication). During 1976–77, near the middle of the period of rapid decline of bison in the mid- to late 1970s, the estimated total loss to the adult and subadult cohorts of the bison population was 191 animals, of which 75 (39%) were caused by hunting and 60 (31%) were presumed to be caused by winter wolf predation (Van Camp, this publication). Thus, at least 70% of the adult–subadult mortality that year could be accounted for by the combined effects of hunting and winter wolf predation. A 2-year period of selective wolf control was implemented in 1977. However, research was terminated before the full impact of the control program could be determined, and the bison population continued to decline (Jalkotzy 1979). Recreational hunting was discontinued in 1977, but continued hunting pressure by General Hunting Licence holders may have been sufficient to account for the observed decline in the bison population from 1979 to 1983 (Van Camp, this publication). Although predation on SRL bison by wolves may have been lessened through control measures, mortality from hunting continued.

Wolf scavenging of bison might also contribute indirectly to bison mortality. Bison carrion left in the field by hunters would add to the amount of food available to wolves. This could enhance wolf pup production and survival and thereby increase predation pressure (Van Camp, this publication). Also, hunting of bison by humans was often selective for calves, yearlings, and young cows; therefore, fewer young animals entered the population and total reproductive potential could decline as the proportion of breeding animals declined (Van Camp and Calef, this publication).

Diseases and parasites are significant causes of mortality in northern bison populations (Fuller 1962, Choquette *et al.* 1972). In addition to causing direct mortality, diseases can also enhance animal susceptibility to predation (Broughton, this publication). It has not been possible to determine the extent to which diseases have limited bison populations in the SRL and WBNP. However, diseases are considered to be one of the major factors contributing to the decline of the SRL bison population. Tuberculosis and brucellosis have been identified in bison in both WBNP and the SRL (Broughton, this publication). Tuberculosis infection rates averaged 40% in WBNP and varied between 25 and 40% in the SRL. Brucellosis infection rates averaged 30% in WBNP and 38% in the SRL. In terms of feed efficiency, weight gain, and milk production, livestock infected with tuberculosis lose an estimated 10–25% of their productive capacity (Blood *et al.* 1983). Brucellosis causes abortion and infertility in cattle (Choquette *et al.* 1978). It can be expected that these diseases have similar effects on bison in the SRL. For example, the 23% drop in pregnancy rate of bison that was recorded at Grand Detour from December 1964 to March 1965 may have been caused specifically by brucellosis infection (Broughton, this publication); however, conclusive data in support of this theory are not available. The presence of brucellosis in wildlife also complicates attempts to raise cattle in contaminated areas and imposes a threat to public health in areas where recreational hunting is permitted.

Numerous outbreaks of anthrax have occurred in the SRL since 1962, with the most recent in 1978. From 1962 to 1978, approximately 1600 bison in the SRL and WBNP have died as a result of anthrax and associated control measures. Anthrax forms spores that reside in the soil. It probably cannot be eradicated from the area and will remain a significant and serious public health threat in the SRL.

Native vegetation in the SRL displayed marked seasonal changes in quality and had high but variable yield (Reynolds and Peden, this publication; Reynolds and Hawley, *Seasonal variation in forage quality*, this publication; Pringle, this publication). The quantity of vegetation produced in the SRL did not appear to limit bison production (Reynolds *et al.* 1978). However, quality of the vegetation was low throughout the winter and snow cover could exclude potential feeding areas (Reynolds and Peden, this publication; Reynolds and Hawley, *Seasonal variation in forage quality*, this publication; Pringle, this publication). Calving rates in WBNP (Fuller 1955) and the SRL (Van Camp and Calef, this publication) could be affected by poor winter nutrition. Older population structure and diseases are two possible contributing factors to late or absent oestrus in the SRL bison herd. However, bison in the MBS have been highly productive on northern native range that is subject to seasonal cycles in vegetation quality that are assumed to be similar to those in the SRL.

The additive effects of hunting, wolf predation, and diseases have decimated free-ranging bison in the SRL. It has not been possible to thoroughly quantify the net effects of individual factors nor has the variation within a factor been determined. However, it seems certain that hunting, predation, and diseases must be controlled if the bison population in the SRL is to increase. Even if those factors are controlled, many years will be required before that population can recover to former numbers and vigour.

2. Cattle ranching

There is considerable public interest in establishing beef cattle ranches in the SRL (Reynolds and Hawley, *Introduction*, this publication). The extensive meadows of the SRL have long attracted the attention of people with desires to develop the area for production of crops and beef cattle. The SRL give the impression of being well suited to commercial ranching because the area is large and undeveloped; the soil is fertile and stone-free; open and fairly level meadows exist, making immediate clearing unnecessary; native forage production is high compared with many southern rangelands; and a local labour pool is available. However, a number of factors conspire to make agricultural development inadvisable.

The availability of large quantities of undeveloped land in the SRL is attributable to the northern location and to the isolation of the area. Land values would likely increase if development occurred. However, existing agricultural market conditions in Canada are such that high transportation costs associated with the northern location outweigh the need for more arable land. Large-scale cattle production would have to compete in distant markets to be profitable, and animals and carcasses would have to be transported at high costs (Pringle, this publication). High transportation costs would have to be offset by low production costs if cattle ranching was to be economically viable. This is not likely to be the case.

If a ranching industry were developed, feed would have to be produced within the SRL to avoid the high cost of import. However, cattle ranching could not be based entirely on the use of the existing forage resource (Pringle, this publication). The productivity of native vegetation is high but variable (Reynolds and Peden, this publication; Pringle, this publication). Wet meadows (predominantly sedge or sedge/grass mixtures) would be more useful for hay production than dry meadows because yields are greater, declines in production associated with continued cutting are less, and forage quality is generally higher. However, the crude protein content of hay from wet meadows in the SRL dropped from 12% in June to 7% by August (Reynolds and Hawley, *Seasonal variation in forage quality*, this publication). Hay prepared from sedge meadows must be harvested early in the growing season to ensure adequate quality (Reynolds and Hawley, *Seasonal variation in forage quality*, this publication; Hawley, this publication; Pringle, this publication; Appendix 1). Early harvest will augment forage quality but there are technical problems associated with harvesting hay from wet meadows. Those meadows are susceptible to flooding and could be wet at the optimum time for harvesting, thereby hindering or preventing the harvesting of hay (Pringle, this publication). Special machinery for harvesting and drying forage from wet meadows could be acquired but at high costs. Ensiling is an alternative method of storing forage but may not be suitable in the SRL because of extremely low winter temperatures.

There is little or no potential for grazing of cattle on the SRL range in winter because environmental conditions are too severe and forage quality is too low (Reynolds and Hawley, *Seasonal variation in forage quality*, this publication). Considerable amounts of supplemental feed and shelter are required to overwinter cattle in the far north (Pringle and Tsukamoto 1974). Long winters in the SRL limit the average grazing season for domestic livestock to 4 or 5 months and require the housing of animals for many months of the year (Pringle, this publication). Range use by cattle would be further limited by harassment from insects (Appendix 1) and it would probably be necessary to provide protection from biting flies. Providing protection by housing in summer would require supplementary feed in addition to the already high requirement for winter feed. More effective use of the range could be made if cattle could be efficiently protected from insect pests (Haufe 1980, Fredeen 1985).

A carrying capacity for the SRL of between 110 000 and 160 000 cows was based on the requirement to supply five times as much cultivated hay as native hay (Pringle, this publication). Early frosts and the short growing season prevent the maturation of cereal grains in the SRL but the potential is good for production of both green feed and forages, such as alfalfa and brome grass (Pringle, this publication). Production could be increased with the use of fertilizers but at additional cost. Variable rainfall causes high yearly fluctuations in forage yield. Irrigation could help but at great cost. Soil salinity would adversely affect domestic crop production in about 10% of the area (Pringle *et al.* 1975). Problems of excessive salinity might develop if the intensity of cultivation were increased. Irrigation and improved drainage could reduce problems with soil salinity but at considerable expense.

Developing the SRL for agriculture would require considerable capital and other investments, by both private enterprises and government. Cattle ranches in the SRL would have to be large, well financed, and well managed (Pringle, this publication). Low input, *ad hoc* production schemes do not appear feasible except at a subsistence level. Access to the SRL is mainly via the Slave River or by air at present. Development of a cattle ranching industry would require construction of suitable roads, infrastructures, and establishment of social service programs that would require large government expenditures at the onset. There is a high risk that additional government subsidies would be required to support and maintain commercial cattle ranches in the SRL (Young 1978). Although not clearly identifiable as costs or benefits, large environmental and social impacts could be expected as a result of development.

Free-ranging bison and conventional livestock production are not compatible. Wild bison would likely destroy fences, depredate feed supplies, and spread diseases. The disease factor is especially important because cattle are susceptible to brucellosis and tuberculosis, and the threat of infection from free-ranging bison would always be present. Vaccination is effective in controlling anthrax in cattle (Blood *et al.* 1983), but control of anthrax would remain a major concern for animal health even if bison were removed from the SRL.

Exclusion of bison from the SRL for the purpose of cattle ranching would be extremely expensive and may be impractical because the animals have been widely dispersed throughout the region since the 1940s (Reynolds and Hawley, *Introduction*, this publication). Free-ranging bison and wolves would remain a threat to cattle ranching even if those species were controlled in the SRL. Although there is little known movement of bison across the Slave River (Calef and Van Camp, this publication), such movement has occurred in the past and recent reports indicate that it continues (C. Gates, pers. commun.). In any case, bison in WBNP would remain a reservoir of disease for the SRL. Wolves have killed many bison in the SRL (Van Camp, this publication) and could be a serious predator of free-ranging cattle (Roy and Dorrance 1976). Wolf control would probably be necessary in any scheme for intensive ungulate production in the SRL; nevertheless, WBNP would remain a source of immigrant wolves (Calef and Van Camp, this publication; Van Camp, this publication).

If the SRL could be agriculturally developed on a large scale, the benefits would include profits to private enterprises, diversification of the economic base, and an increase in the number and diversity of jobs. Initially, jobs would be created for unskilled local labour, but local residents would be able to contribute more with the acquisition of requisite skills. However, those potential benefits may not be viewed as an improvement in life style by local residents, whose traditional sources of income are hunting, trapping, and guiding, or by conservationists, who value and strive to maintain wilderness land.

Raising cattle on a large scale in the SRL would have a great environmental impact through major developments such as roads and infrastructures and would seriously affect the existing biological system. Considerable financial, technical, and managerial expertise would be required and would probably have to be imported from the south. At the same time, traditional sources of livelihood of many native residents would be undermined. A strong desire to harvest bison has developed over the years among many of the residents from Fort Resolution, Fort Smith, and other nearby communities. Those people have hunted bison in the SRL for meat over the last several decades (Boreal Ecology Services Ltd. 1982). It cannot be assumed that participation in cattle enterprises would be desired by residents or would be viewed by them as an improvement in their life styles. Any decision to encourage cattle ranching in the SRL must acknowledge that certain environmental and sociological changes will likely occur in the region from such development. Although cattle ranching in the SRL is technically feasible, there are economic, biological, sociological, and epidemiological factors that militate against that type of development.

3. Other ranching options

Bison may be the species best suited for production in the SRL. They appear to be better adapted to the SRL environment than Hereford cattle (Hawley *et al.* 1981*a* and *b*). Bison have a greater cold hardiness (Christopherson *et al.* 1976) and can digest lower quality native forages better than cattle (Hawley *et al.* 1981*a* and *b*). Bison–cattle hybrids have a greater capacity for winter foraging than do purebred cattle (Smoliak and Peters 1955), a trait likely attributable to the influence of bison genes. Bison may also be able to seasonally adjust their metabolic rates (Christopherson *et al.* 1979), a trait that would enhance survival during periods of nutrient deprivation in winter. These differences reflect differences in selective pressures that have moulded the two species: bison evolved as wild animals under natural environments, whereas cattle were selected for production under less severe environmental conditions. Thus, bison possess the potential to be more productive under harsh natural environmental conditions typical of the SRL.

There are two approaches that could be taken to enhance bison production in the SRL. One strategy involves more intensive application of traditional wildlife management practices to increase existing populations of wild ungulates, primarily bison. The second involves the commercial production of bison and perhaps other species in confined mixed-species grazing systems. Some residents of the area are interested in these alternatives to cattle ranching. For example, in 1982 the Fort Smith Hunters and Trappers Association requested the Northwest Territories (NWT) government to commission a study into the feasibility of establishing a disease-free bison herd in the SRL (Boreal Ecology Services Ltd. 1982). The conclusions of that study were that sufficient habitat for a new bison herd exists without causing displacement of the Hook Lake population, management and control of disease are possible in an isolated bison population, and the NWT Wildlife Service should review the implications of establishing a disease-free bison herd in the SRL. Further studies being conducted for the Hunters and Trappers Association to determine economic viability of bison ranching in the SRL are nearing completion.

The SRL bison population was at one time estimated to be in excess of 2000 but is currently much smaller. Only a small portion of available range is now being used. Therefore, in terms of carrying capacity of the forage, it should be possible to increase bison numbers above the current level. Limitations to this approach were discussed earlier in this paper. Among them are requirements for control of hunting, predation, and disease. Successful intensive management of bison as a wildlife resource would lead to economic benefits for the region, including increased revenues from hunters and an increased supply of game for residents of the NWT. The non-economic benefits arising from that scheme would include minimal environmental disruption and continuation of traditional life styles for local residents.

The inability to effectively control disease in the SRL bison herd, as illustrated by earlier failures (Broughton, this publication), would be a significant limitation to production of wild bison. Control of tuberculosis and brucellosis might be accomplished by a rigorous and expensive testing and slaughter program. Anthrax cannot be eradicated by such methods but might be controlled with an annual vaccination program. Testing and vaccination programs require corral facilities and the assembling of animals and, to be successful, all animals must be subjected to tests and vaccinations. Inoculation of the majority of animals would be difficult because wild bison are scattered in small groups throughout the range (Calef and Van Camp, this publication). That difficulty contributed to termination of the inoculation program at Hook Lake in 1975 (Broughton, this publication). If disease control programs are reinstated in the future, they should strive to contain additional outbreaks and prevent the spread of diseases by selective slaughter of reactor animals. Eradication of tuberculosis and brucellosis from the SRL bison population might not be possible without extermination of the existing bison and re-introduction of disease-free animals; however, this would not eradicate anthrax.

Commercial production of bison and other species in mixed-species grazing systems would be a new approach to animal production in the SRL. Mixed-species grazing systems are based on the assumption that maximum use of the

Table 1
Theoretical comparison of three animal management strategies for increasing ungulate production in the Slave River lowlands (Comparison assumes that resources are managed to optimize production.)

	Strategy		
Characteristic	Conventional cattle ranching	Intensive wildlife management	Wild or feral mixed-species grazing
Potential for meat production	high	low	intermediate
Energy and capital requirements	high	low	high
Response to range improvements	high	low to intermediate	intermediate
Infrastructure and service requirements	high	low	intermediate
Compatibility with existing land use	low	high	intermediate
Compatibility with native land use interests	low	high	intermediate or high
Requirements for legislative changes	intermediate	low	high
Employment of unskilled labour	high	low	intermediate
Detrimental effects of insect pests	high	low	intermediate
Compatibility with Wood Buffalo National Park	low	high	intermediate
Requirement for predator control	high	intermediate	intermediate or high
Cost of winter maintenance	high	low	intermediate
Difficulty of disease control	low	high	high
Environmental impact caused by development	high	low	unknown
Fluctuations in production	low	intermediate to high	unknown
Severity of climatic restraints to development	high	low	intermediate or low

forage resource can be achieved by grazing a combination of herbivores that are largely non-overlapping in forage selection and non-competitive in other ways. Systems using wild animals have a minimum requirement for supplemental feed and animal shelter, can exert a minimum environmental impact, and involve minimum resource development compared with systems using domestic livestock. However, problems associated with harvest of animals and control of diseases would be much greater in mixed-species systems than in production systems using single species or in conventional cattle ranching schemes.

To determine the potential for commercial bison or mixed-species ranching, additional information is required on intensive management strategies for bison, harvest potentials, dollar values of marketable animal products, and the size and location of commercial markets. Future research should be directed toward these areas. However, potential problems identified for development of a cattle ranching industry, such as the need for infrastructures and markets, a possible requirement for government subsidy, and the need for managerial expertise from outside the region, would also be problems for development of a bison ranching industry.

Feral horses have been discussed as an alternative for meat production in the SRL (Pringle, this publication). Both feral horses and bison have demonstrated their adaptability for survival in northern habitats, they possess the ability to use low quality forage, and they are able to cope with adverse environmental conditions. However, free-ranging horses may have a greater detrimental impact on the range than other herbivore species. The potential for raising horses in a grazing system on a commercial scale should be investigated. Elk and moose should also be evaluated to determine their potential for mixed-species production strategies in the SRL.

High costs of transportation from northern locations would be a problem for any animal production enterprise. However, meat and by-products from wild or feral animals tend to be specialty products that have high values, and there are sizable foreign and domestic markets for these products. For example, bison meat is a specialty item in North America and has a dollar value that is usually 1.3 to 1.5 times that of beef. In a mixed-species system involving bison, additional revenue could be generated from the sale of by-products such as heads, hides, skulls, and horns, or from trophy fees to harvest animals by hunting.

The three animal management strategies for increasing ungulate production in the SRL are compared on a theoretical basis and on a relative scale in Table 1. The comparisons are based on characteristics deemed relevant to the SRL; in most ways, the mixed-species grazing strategy, a multi-resource use concept, is intermediate to the production strategies of conventional cattle ranching and intensive wildlife management.

Enhancing ungulate productivity in the Slave River lowlands

Alexander W.L. Hawley
Hal W. Reynolds

Hunting by humans, predation by wolves, and diseases are the three major factors that have caused the decline of the SRL bison population. Any attempt to enhance animal productivity in the SRL will require control of those factors; however, it is uncertain to what extent control is possible.

There is a spectrum of management alternatives that could be applied to the SRL, ranging from maintenance of the status quo through intensive bison management and mixed-species farming to large-scale agricultural development. Maintenance of the status quo seems unacceptable because the desire of residents for enhanced animal productivity in the region was specified as one of the main reasons for establishment of this cooperative study. However, it is not certain at this time that feasible management alternatives are available to enhance production significantly.

A wildlife management strategy involving predator control and regulation of hunting could be implemented in an attempt to improve production of wild bison. The major limitation to enhancing production with this strategy would be the presence of diseases in bison in the SRL and WBNP and the problems associated with effective control of those diseases. Enhanced bison production in the SRL may not be possible without extermination of the resident bison and reintroduction of disease-free animals. Even then, bison in WBNP would serve as a reservoir of disease. Furthermore, vaccination of bison and slaughter for disease control would not remove the threat of anthrax.

Intensive farming of confined animals would permit better control of disease, but economic, epidemiological, biological, and sociological factors are arguments against cattle ranching in the SRL. The prospect of producing cattle cheaply and on a large scale in the SRL because of the large quantity of inexpensive forage is a dream that cannot be realized. Furthermore, domestic animal agriculture, at any level other than subsistence, would require extensive regional development and would conflict with current land uses and desires of local residents. Free-ranging bison and conventional livestock operations are not compatible because wild bison are likely to spread disease, destroy fences, and depredate feed supplies. Even if extensive agricultural development were to occur in the SRL, WBNP would remain a continual source of immigrant wolves and bison. The wolves would likely prey on cattle and the bison would harbour disease. Previous studies were unable to recommend agricultural development in the SRL. Similarly, agricultural development of the SRL is not supported by the present studies.

Commercial production of captive bison alone or in combination with other large mammals is an alternative for enhancing animal production. That approach would capitalize on the potential for control of diseases and predators afforded by maintaining captive animals while taking advantage of the hardiness and productive advantages of wild animals that are better adapted to harsh environmental conditions. The practicality of a mixed-species grazing system in the SRL and the economics of game ranching need to be studied before the efficacy of those approaches can be evaluated. A pilot study ranch may be required in the SRL to fully assess the feasibility of producing wild or feral species commercially and to develop management practices and recommendations for a mixed-species grazing system. Bison should be the primary species in the project because they are native to the area, they have previously demonstrated productivity in the SRL, they are adapted to the northern environment, and they are a species desired by local residents. Horses also warrant investigation because they may be suitable for a minimal management strategy. The pilot project should be conducted as a commercial enterprise with research emphasis on financial and production aspects. Project personnel should have some knowledge of raising animals for meat commercially and understand the special requirements of handling wild animals. Legislative changes required to accommodate commercial production of wild species should be investigated, including the formulation of regulations to permit handling and sale of animals that are legally classified as wildlife. The socioeconomic aspects of proposed commercial production systems for wild game should be investigated and discussed with local residents. Also, the public sector and special interest groups, such as native bands and wildlife associations, should have input into the development of a land-use policy for the SRL.

In the interim, a wildlife management policy to improve production of the existing SRL bison herd should be implemented with the primary aim of providing more bison for use by local residents in line with current desires and demand. Management strategies presently available to achieve that goal include regulation of hunting and control of predators. Diseases of resident bison are a major limitation to any animal production strategy that will extend beyond the status quo. Without control of diseases, the threat of contamination in the SRL remains high. Management strategies designed to significantly increase bison productivity as a wildlife resource, to commercially produce bison under intensive ranching operations, or to involve bison in mixed-species grazing systems will not be feasible in the SRL until the disease problem has been rectified.

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Appendices

Appendix 1
Cattle farming by the Oblate missionaries in the Slave–Mackenzie River corridor[1]
by A.W.L. Hawley

The Oblate missionaries established eight mission farms along the Slave–Mackenzie river corridor between Fort Chipewyan and Aklavik. Although primarily devoted to vegetable production, several farms maintained cattle; however, little information on the level of cattle production is available. St. Bruno's farm, the primary site of beef production for all the missions, was established in 1910 between Fort Smith and the Salt River, Northwest Territories, south of the Hook Lake study area. Duchaussois (1937) reported that up to 100 cows were held at St. Bruno's farm, but other sources reported that as many as 170 head of cattle, most of them Herefords, were held there during the 1920s. At least three mission farms maintained cows for milking; about 10 cows were kept at Fort Chipewyan, 5–6 cows at Fort Simpson, and 8–10 cows at Fort Resolution.

Native hay was the primary cattle feed and was usually harvested with horse-drawn mowing machines. Hay was harvested by hand in some years because extensive flooding prevented the use of horses and light machinery. "Red-top" grass (*Calamagrostis* spp.) was harvested as hay in early July. It was used to feed horses but was not readily consumed by cattle. The cattle were fed sedge hay (*Carex* spp.), which was harvested in late July. It was critical to harvest sedge hay before the end of July because later phenological stages were considered to be too "dry" and "hard" to be suitable cattle feed.

Beef cattle were fed hay exclusively whereas milk cows received grain and vegetable mash as feed supplements. None of the mission farms, with the possible exception of Fort Simpson, had sufficient meadows nearby to meet the hay requirements of their livestock. Hay was often transported from 80 or 100 km from harvest sites.

Foraging by livestock was made difficult by biting flies. Mosquitoes (Culicidae), black flies (Simuliidae), sand flies (Ceratopogonidae), and horse flies, or bulldogs (Tabanidae), all caused serious problems, with bulldogs generally inflicting the greatest harm. Harassment from biting flies kept cattle close to farm shelters in spite of the absence of fencing. During much of the summer, livestock could be pastured only if there were strong winds or low temperatures to reduce harassment from insects. Some barns were equipped with screen doors and it was often necessary to provide horses and cattle with smudge fires. Inadequate protection against insects led to weight loss and fatigue in cattle. Insect bites around the eyes would occasionally cause severe swelling and blindness in cattle.

Horses were necessarily exposed to flies during the harvesting of hay. To provide some protection from insects, horses were coated with a mixture of pine tar and tallow and were completely covered with canvas smocks. Temporary shelters were built at each harvest site and smudge fires were used to provide the horses with overnight protection from flies.

Most farming by the Oblate missionaries has since ceased. The primary reasons for closure of the mission farms included a decline in the number of personnel available to work on the farms and the increased availability of produce from southern Canada. The introduction of bison from Wainwright to Wood Buffalo National Park also contributed substantially to the closure of St. Bruno's farm in 1928. Most of the hay required to feed cattle at St. Bruno's was harvested on the west side of the Salt River adjacent to the park. This hay was stacked and stored at the harvest site and hauled daily to the farm during winter when horses with sleighs could traverse the usually marshy ground. The continual destruction of these stacks by the introduced bison was a major factor contributing to closure of St. Bruno's farm. The mission at Fort Smith continued to maintain a few milk cows until the mid-1950s, when they were slaughtered because a blood test had revealed brucellosis in the herd (Wm. Fuller, pers. commun.):

[1] Most of the information was obtained through personal communication with Brothers Henry Sareault, Joseph Brodeur, and Joseph Laplante, Fort Smith, Northwest Territories, 1978.

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