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WILDLIFE MANAGEMENT BULLETIN

The Biology and Management of The BISON of Wood Buffalo National Park

by
William Albert Fuller

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OF WOOD BUFFALO NATIONAL PARK

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Canadian Wildlife Service
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The Honourable Walter Dinsdale, P.C., M.P.,
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Introduction

The investigation that forms the basis of this report was the direct outgrowth of the discovery of tuberculosis in the bison of Wood Buffalo National Park in the years 1947 to 1949. The object of the study was to formulate a management plan for the infected herd. To accomplish this, it was necessary to know the incidence of tuberculosis and whether or not the incidence varied from one locality to another. It was also necessary to learn something of the population dynamics of the bison. The rate of reproductive gain was accordingly studied in considerable detail. An excellent opportunity to study certain aspects of reproduction was presented at the annual slaughters from 1952 to 1956. Calf ratios were studied in the field by making frequent calf counts along the park trails or from low-flying aircraft. Mortality factors were studied also, both in the field and at the annual slaughters. The presence of a qualified veterinarian at the slaughters allowed the recognition of several disease conditions which otherwise might have been overlooked.

The study really began in 1950, although as early as 1947 the writer had examined a few specimens and in 1949 made an aerial census of the bison, including those just outside the park boundaries (Fuller, 1950). From 1950 to 1956 extensive herd observations were made along the park roads and trails and from the air in an attempt to understand such factors as calf production and survival, social organization, and relations with predators. At the annual slaughters from 1951-52 to 1955-56 about 1,800 carcasses were examined. An additional 65 bison were killed for miscellaneous reasons or were found dead during that period.

Many persons assisted in a variety of ways in the completion of the study. Thanks are especially due to E. H. Essex, former Superintendent of Wood Buffalo National Park, for courtesies too numerous to mention. W. G. Brown and L. A. C. O. Hunt, District Administrators at Fort Smith during the course of the investigation, assisted greatly. The assistance of the following is also appreciated: C. R. Slater, G. A. West, N. S. Novakowski and R. C. Stewart, all student field assistants; W. G. McNeill and John Tourangeau of Fort Smith; and Rod Fraser of Fort Chipewyan. The manuscript was read critically by Drs. R. A. McCabe, J. J. Hickey, and J. T. Emlen Jr. of the University of Wisconsin and Dr. A. W. F. Banfield and other members of the staff of the Mammalogy Section of the Canadian Wildlife Service.

Historical Summary

Preble (1908), Raup (1935), and especially Soper (1941) published detailed summaries of early exploratory work in the general region of the present Wood Buffalo National Park. It is only necessary to recapitulate here the events dealing directly with the preservation of the bison and to complete the account from 1934 to the present.

Seton (1929) assigned to the bison living in the woods an area of 1,000,000 square miles and a primitive population of 5,000,000, implying a carrying capacity of five bison per square mile. The narratives of the early northern explorers, however, do not support that estimate. Preble (1908) presented a concise but adequate review of early historical accounts. From Hearne in 1772 to Pike, Russel, and Whitney in the 1890's, all reports indicated an uneven distribution and a general scarcity of bison. During that time almost the only Europeans in the country in addition to the explorers were a few fur traders, so the scarcity cannot be ascribed to the influence of the white hunters as it was in Southern Canada and the United States.

In 1893 the Canadian parliament enacted legislation providing complete legal protection for the remnant herd of wild bison, estimated to number not more than 500. Enforcement of the regulation was entrusted to the Royal North West Mounted Police until 1911, when six "buffalo rangers" were appointed. Their sole duty was to patrol the bison range and protect the animals from poachers.

In December, 1922, Wood Buffalo National Park, encompassing an area of about 10,500 square miles, was created by Order in Council. At that time the bison population was estimated by Graham (1923) to number 1,500.

The next two developments go hand in hand. First was the controversial introduction of 6,673 plains bison from the Buffalo Park at Wainwright, Alberta, in the years 1925 to 1928. As early as 1926, an estimated 400 bison, thought to be mainly animals introduced in 1925, had invaded the lush meadows of the Peace River delta, outside the park boundaries. Immediate steps were taken to enlarge the park to its present size of 17,300 square miles. The wisdom of that step is apparent, for today those meadows support a minimum of 4,000 bison the year round.

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In the summers of 1928, 1929, and 1930, H. M. Raup conducted botanical investigations in the park. His work resulted in two important publications dealing with range conditions (1933) and general botany (1935).

From 1932 to 1934, J. Dewey Soper was commissioned by the Lands, Parks and Forests Branch of what was then the Department of Mines and Resources, to undertake a study of the bison. The results of his work are embodied in his excellent monograph (1941), and several lesser papers (1937, 1939, 1942). He estimated the bison population in 1934 to be between 10,000 and 12,000.

In 1934 Colonel Harry Snider of Calgary and George Goodwin of the American Museum of Natural History visited the park and secured habitat groups of bison for the National Museum of Canada and the American Museum. A semi-popular account of their expedition was published by Goodwin (1935).

J. Dewey Soper spent three months in the park in the spring of 1945. His lengthy unpublished report (1945) dealt mainly with the question of wolf predation. In February, 1949, the writer made an aerial census of the bison in the park and vicinity (Fuller, 1950) and estimated the population to be between 10,000 and 12,500 at that time. A second census was made in 1951, the results of which were in close agreement with the 1949 result (Fuller, 1951, unpublished MS in files of Canadian Wildlife Service). At the commencement of the present study, therefore, the bison population had apparently been stable for a period of 15 to 20 years.

Taxonomy

The weight of scientific opinion has always favoured the view that the "wood" buffalo was at least subspecifically distinct from the "plains" animal. Allen (1876), Seton (1886), Rhoads (1898), Rowan (1929), and Skinner and Kaisen (1947) have all taken this stand, whereas Hornaday (1889) and Garretson (1938) have been the most noteworthy dissenters. Of the list only Seton and Rowan had first-hand knowledge of the living animals. Rowan also claimed familiarity with the wisent of Europe (*Bison bonasus*) and held that the "wood" buffalo was intermediate in certain characters between it and the "plains" bison (personal communication). Rhoads (op. cit.) in describing the "wood" buffalo as a subspecies, *Bison bison athabascae,* voiced the suspicion that it might be a more primitive race than *Bison bison bison,* thus anticipating Rowan's remarks and supporting Seton who made the suggestion in 1886. The opposing argument was that the "wood" buffalo were "plains" animals that had retired to the shelter of the woods and that any slight differences in appearance they might have acquired were "largely owing to environment" (Graham 1923). That argument presupposes that the "plains" type was ancestral to the wood buffalo. The careful and detailed work of Skinner and Kaisen (1947) should have ended the controversy once and for all. They showed by a direct comparison of a large series of specimens, that there are consistent differences in cranial characteristics sufficient to establish *Bison bison athabascae* as a valid subspecies. Furthermore, they held that *athabascae* is closer to the extinct, ancestral form, *Bison occidentalis,* and that *athabascae* is also the proper name for the so-called "mountain" buffalo, which formerly extended into Oregon, Colorado, and Wyoming. In the face of this, it is curious to note that Roe (1951) adduces a mass of evidence which supports the distinctness of the northern wood buffalo, but at the same time purports to show, on the basis of historical accounts, that the mountain buffalo was smaller, not larger, than the plains animal and, therefore, could not be identical with the wood buffalo. In settling this taxonomic question, measurements must receive priority over "eye-witness accounts" of the early plainsmen.

Graham (1923), upon whose recommendation Wood Buffalo Park was established, estimated the population of wood buffalo in 1922 to be 1,500 head.

In view of the difficulties in taking an adequate census before the advent of the aeroplane, the best that can be said for that figure is that it was an intelligent guess and entirely within the bounds of possibility. It seems safe to assume that the population was between 1,000 and 2,000 at that time. During the four years of the transplant, (1925 to 1928), the official records show that just over 6,600 plains bison were liberated at two or three selected spots, all within a few miles of each other, along the Slave River. This meant that the imports outnumbered the originals by about four to one, if Graham's estimate was approximately correct.

Reports of the wardens assigned to follow some of the new releases are replete with examples of immediate acceptance of one race by the other. Cross-breeding was reported to have occurred during the first year, and over most of the range has been going on for 30 years. The original preponderance of plains animals has resulted in the virtual disappearance of the pure wood buffalo.

There are, however, in the inaccessible northwest quarter of the park, small herds of bison which may be pure or nearly pure *athabascae*. No natural travel lanes link that area with the remainder of the park, which has been taken over by hybrids. Conclusive evidence will have to await the penetration of the area by a motor road. Until such a road is completed, the area will remain as impenetrable as it was in 1907 when Seton and Preble were forced to turn back before reaching the bison range (Seton, 1911).

The animals that are the subject of this report, then, are hybrid *Bison b. bison* $\times$ *B. b. athabascae,* with a preponderance of progenitors (and hence of genetic characteristics) of the former type.

The Bison Range

The physical and biotic features of the bison range are important, particularly in relation to the distribution and seasonal movements of the bison. An attempt is made in this section to describe briefly the physical and biological environments found in Wood Buffalo Park. More complete accounts may be found in Raup (1933, 1935) and Soper (1939, 1941).

Physical Features

Wood Buffalo Park (P. 53) lies wholly within that northward extension of the Great Central Plain known as the Mackenzie Lowlands. That formation has the shape of an elongated triangle, with its main axis lying in a southeast-northwest direction. Its base extends from west-central Alberta to northeastern Alberta, and its apex lies on the shore of the Arctic Ocean, where it consists solely of the delta of the Mackenzie River. The east and west boundaries of the triangle are rather sharply defined by the Laurentian Plateau and the Cordillera, respectively. The park lies within the triangle, about one-third of the distance along the main axis from the base, and has for part of its eastern boundary the line of contact between the lowlands and the Laurentian Plateau. In terms of map co-ordinates, it extends from approximately latitudes 58°10′N. to 60°30′N. and from 111°30′W. to 115°30′W. longitude.

The topography of the park has been described by Raup (1933) and Soper (1939), both of whom recognized four elevations. The highest of them is represented only by portions of the Caribou and Birch Mountains, which are erosion plateaus of Cretaceous age. They are thought to have modified the course of the advance and retreat of the Keewatin ice sheet, but are unimportant today as bison range either actual or potential. Caribou Mountain reaches a height of more than 3,000 feet and Birch Mountain about 2,700 feet.

The second level, the Alberta Plateau, probably corresponds to the third prairie steppe (Soper, 1939). It is most developed north of Peace River where it forms a broad, relatively flat upland 800 to 1,000 feet above sea-level, sloping

gently eastward from the base of Caribou Mountain. The central portion of the Alberta Plateau is a shallow depression filled with many swampy lakes. Its surface is otherwise featureless save for chains of low, rounded hills, generally not more than 100 feet high, all of which seem to have been derived from glacial moraines. Drainage of the Alberta Plateau is poorly developed, with the result that many bogs occur, particularly in the central depression. The gypsiferous terrain along the eastern margin, and the morainal hills, however, are dry and are important summering areas for the bison.

The next level, commonly known as the Salt Plains, is probably related to the second prairie steppe. It has an elevation of 700 to 800 feet, and is separated from the Alberta Plateau by a prominent limestone escarpment. North of the Peace River to about the 60th parallel it is found in a strip 15 to 20 miles wide between the limestone escarpment and the Slave River lowlands. That level is also found extensively south of Peace River to the west of Lake Claire. North of Peace River, the Salt Plains are a major wintering ground, whereas south of Peace River and west of Lake Claire the corresponding elevation is little used by bison.

The fourth and lowest level is the alluvial lowlands of the Athabasca-Slave-Peace Rivers system. The combined delta of the Peace and Athabasca Rivers west of Lake Athabasca is the largest alluvial area in the park. The northern or Peace River portion of the delta is also the finest range in both summer and winter and carries approximately one-third of all the bison the year round. North of 60° another extensive alluvial flat lies between the Slave and Little Buffalo Rivers. It provides winter range for another significant part of the herd.

In summary, the park, in keeping with the entire Mackenzie Lowlands, has a gradual slope from south to north on which is superimposed a slope from west to east in four more or less definite steps.

The recent geological history of the park has been described in detail by Cameron (1922). From a study of ancient beach lines he described four post-glacial lake expansions, which, at one time or another, covered all of the Alberta Plateau and Salt Plains elevations. The low morainal hills, previously mentioned, are other important products of glaciation.

The soils of the entire region were derived directly from either the systems of moraines or the post-glacial lake bottoms, or from subsequent deposition by the major rivers in the lowlands. The later fluvial deposits are the richest soils in the park and support dense stands of white spruce (*Picea glauca*). The soils of the Salt Plains are clayey, in general, but, as the name implies, outwash, from the brine springs at the base of the escarpment which marks their western edge, has left thin deposits of salt (NaCl) in many depressions.

The soils of the Alberta Plateau are predominantly light, with large amounts of sand and gravel. Raup (1935) describes two areas where there is a significant

admixture of clay, producing a heavier soil. They are in a narrow zone at the eastern edge of Caribou Mountain, and in the Pine Lake-Flatgrass Lake area. The former is at present little used by bison, but the latter forms some of the finest summer range in the park.

Climate

The climate has been adequately described by Raup (1935) and Soper (1941). It is characterized by long, cold winters; short, but hot summers; and little precipitation, nearly half of which falls as snow. The climatic conditions are recorded in Tables 1 to 4, which are summarized weather records from three

Table 1. Average temperatures (°F) at three stations near Wood Buffalo National Park

		Embarras (1945-54)	Fort Smith (1945-54)	Resolution (1946-54)
Mean daily max.	Jan.	— 1.5 (—17.1 to 13.8)	— 7.8 (—21.3 to 5.4)	— 9.4 (—19.2 to 3.7)
	July	75.0 (71.4 to 77.9)	73.8 (70.9 to 76.0)	69.1 (65.9 to 71.0)
Mean daily min.	Jan.	—21.7 (—8.5 to —40.2)	—27.2 (—14.9 to —41.6)	—25.5 (—13.8 to —34.9)
	July	50.8 (48.8 to 53.1)	47.0 (44.5 to 50.6)	50.5 (48.4 to 53.1)
Absolute min.		—59.8	—65.0	—56.0
Absolute max.		93.4	93.6	91.6

Table 2. Total annual rainfall (inches)

Place	1945	'46	'47	'48	'49	
Embarras	11.66	12.17	10.90	10.38	10.52	
Fort Smith	—	7.08	—	7.45	6.75	
Resolution	—	5.59	5.17	11.28	5.26	
	'50	'51	'52	'53	'54	Average
Embarras	7.71	8.08	10.76	8.80	12.14	10.31
Fort Smith	6.46	6.17	5.54	6.42	8.04	6.74
Resolution	3.71	7.04	6.80	7.68	8.53	6.78

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stations along the eastern park boundary for the decade 1945 to 1954. The data were supplied by the Meteorological Division of the Department of Transport, Toronto, Ontario.

Winter is undoubtedly the most difficult season for bison. Extreme cold *per se* seems to have little effect on them, and they may be seen grazing on prairies in temperatures of —50°F on calm days. Extreme cold coupled with even a moderate wind (over 8 to 10 m.p.h.), however, will send them to the shelter of the woods. Grazing is then confined to a narrow zone around the edge of the prairies, next to the timber. Winds stronger than about 15 m.p.h. are rare in periods of extreme cold. Likewise, a succession of windy days is uncommon in midwinter. Three days is commonly the duration of the most severe winter storms. Since dense woods, which give protection from the wind, are everywhere well interspersed with grazing areas, the bison are secure from the damaging effects of cold, with or without wind. Snow conditions may be of great importance. Heavily crusted snow hinders the animals in their foraging and also makes travel more energy-consuming, thus aggravating the effects of prolonged cold. Fortunately, winter thaws are rare on the bison range. Raup (1933) cites several accounts of a severe thaw and freeze about 1865, which was blamed by the Indians for the marked decrease in bison numbers that occurred about that time. Raup also records a thaw of four days' duration in March, 1928, followed by a freeze that made foraging on the open prairies difficult. A similar condition was observed following a thaw in February, 1954. On the latter occasion, however, the bison were able to break through the crust for foraging, but were noticeably handicapped in moving from place to place. That difficulty is, of course, less serious for a social species than for a solitary one. The bulls were seen to take the lead and break a trail, which the weaker animals followed in single file with much less expenditure of energy.

Table 3. Total annual snowfall (inches)

Place	1945	'46	'47	'48	'49	
Embarras	31.3	45.5	60.7	78.3	70.9	
Fort Smith	—	50.2	—	42.2	56.9	
Resolution	—	76.2	30.4	18.3	43.7	
	'50	'51	'52	'53	'54	Average
Embarras	77.3	64.2	47.9	51.6	40.3	56.8
Fort Smith	48.2	50.0	45.6	69.5	58.5	52.6
Resolution	51.8	76.6	45.5	43.3	33.9	46.6

Table 4. Number of days between last frost in spring and first frost in autumn

Place	1945	'46	'47	'48	'49	
Embarras	72	58	76	88	93	
Fort Smith	65	56	47	86	46	
Resolution	—	108	88	109	91	
	'50	'51	'52	'53	'54	Average
Embarras	79	70	94	108	87	82.5
Fort Smith	*	26	37	28	97	54.2
Resolution	80	104	106	108	119	101.4

*Virtually no frost-free period because of two frosts in July.

The total snowfall in the park may be classed as moderate (Table 3). Typically, most of the snow falls in early winter, chiefly November. Compaction is rapid on wind-blown plains, lakes, and rivers, but is entirely lacking in the shelter of the forests. Drifts up to four feet in depth commonly form around the margins of prairies when wind-driven snow piles up against the brush.

Biotic Environment and Phenology

Since the phenology of the park has been dealt with in some detail by Soper in his 1941 monograph, only a brief summary of major events is presented in this section. Soper points out that the winter is approximately equal in length to the other three seasons combined. Winter may be said to begin with the freeze-up of the major rivers and large lakes between October 25 and November 10. Heavy snow-storms characterize November and early December. The snow packs and crystallizes on the prairies and plains, which are the major bison wintering areas, during the periods of extreme cold which last with only minor breaks from late December to late February. March, as elsewhere, is cold and blustery. The first thaws occur soon after the spring equinox, and the snow may disappear in exposed places by the end of April, while lingering for another three weeks in dense forests and on northern exposures.

Spring begins with the break-up of the rivers, which occurs between May 5 and 15. Catkins may be found on willows (*Salix* spp.) as early as May 1. The ubiquitous pasque flower (*Anemone patens*) blooms about May 20, at which time the leaves of willow, alder (*Alnus* sp.), and aspen (*Populus tremuloides*) are just bursting their buds. Those deciduous species are usually in full leaf by June 10. The telescoping of the seasons is illustrated by the blooming of the prairie flora.

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Some prairie species such as shooting star (*Dodecatheon pauciflorum*) and saline plantain (*Plantago eriopoda*) are at the height of flowering by mid-June. The northern bedstraw (*Galium boreale*), common yarrow (*Achillia millifolium*), and bluebell (*Campanula rotundifolia*) bloom in July, whereas such typical autumn forms as goldenrod (*Solidago canadensis* and *S. oreophila*), the various asters (*Aster* spp.), fringed gentian (*Gentiana elegans*), and pussy's toes (*Antennaria mitida*) bloom in late July or early August.

Colour appears in the leaves of aspen, birch, and viburnum in late August, and autumn colours are at their height by September 15. Most of the leaves have fallen by early October, but the tamaracks lend a touch of colour to the margins of bogs throughout that month.

The fly season begins in late May or earlier with a large species of mosquito which presumably overwinters in the adult stage. "Bull dogs" (Tabanidae) make their appearance in June, and, along with the mosquitoes, render July an almost impossible month for travelling and camping in the bush. August brings an abatement of both of these pests. Black flies (Simuliidae) are not important in the park, probably because of the dearth of breeding sites in fast-flowing streams. Black flies do not become noticeable until August and persist as a minor annoyance well into October. "No-see'ums" (Ceratopogonidae) may be troublesome during the hot, dry weather of late July and early August.

The major vegetative types in the park and their use by bison are shown in summary in Table 5. The area that presently carries the greatest concentration of bison is the extensive delta plain of the Peace River, lying between Peace River and Lake Claire. Those meadows are covered largely with an almost pure stand of meadow sedge (*Carex trichocarpa* var. *aristata*). That species is a staple food of the bison in both summer and winter, but is especially important in the latter season because it cures into hay on the stem and produces a green shoot, rich in stored nutriment. The river flood-plains, abandoned channels, and dry beds of oxbow lakes also contain an abundance of that species, which undoubtedly accounts for their popularity as winter range.

The upland prairies are distinguished from the meadows by their more xerophytic conditions which favour grasses rather than sedges. Blue-joint grass (*Calamagrostis canadensis*), blue grass (*Poa pratensis*), wheat grasses (*Agropyron* spp.), and June grass (*Koeleria cristata*) are common and important food plants. Raup (1933, 1935) describes two areas in which semi-open prairies occur. To these, the writer would add a third that was unknown to Raup and unmapped at the time of his work in the park: the region along the upper Nyarling River and west almost to Copp Lake, seen many times from the air, but never on the ground. That area was obviously Seton's objective on his unsuccessful ascent of the Nyarling (Seton, 1911). Soper (1945) is the only biologist who has ever visited the area, and unfortunately his account contains no details of the vegetation. He

was able to penetrate the area by means of the military road, built as a spur to the Canol Road in 1943, which rapidly fell into disrepair with the termination of the Second World War. It is certain that those prairies have supported bison for a very long time, and it is highly probable that the few hundreds that still live there are wood buffalo (*B. b. athabascae*).

Table 5. Summary of vegetative types in Wood Buffalo National Park and their importance for bison

Vegetative type	Extent	Use by buffalo
Forest		
White spruce	Climax widely distributed on heavier soils	Shelter from winter storms
Jack pine	Edaphic subclimax (?) widely distributed on lighter soils	Shelter, dust wallows, major migratory routes
Aspen	Widely distributed following fire and in early successional stages	Shelter; forest floor contains grasses and legumes, giving some summer forage
Black poplar	Confined to stream banks, particularly delta channels	Very little used
Upland prairie		
Openings in forest	Three chief areas of considerable extent. Probably confined to clayey soils	Important summer range
Salt plains	Long narrow strip along eastern margin of park	Mainly winter range, but also used in summer
Sink holes	Widely scattered in gypsiferous terrain of eastern edge Alberta Plateau	Summer forage in forest areas otherwise lacking in food species
Lowland meadows		
Delta plains	Combined delta of Peace and Athabasca Rivers	Important year-round range
River flood plains	Chiefly along Peace and Slave Rivers	Mainly winter range, but also used in summer
Marshy lake margins	Widely distributed throughout the park, especially Alberta Plateau	Summer forage in forest areas otherwise lacking in food
Muskeg (peat bog)	Widely distributed—many of considerable area	Generally avoided

The Salt Plains prairies, as their name implies, contain a considerable halophytic element in their flora. Such species as glasswort (*Salicornia europaea*), black saltwort (*Glaux maritima*), and arrow grass (*Triglochin maritima*) are abundant around saline depressions and on the margins of saline sloughs and streams, but add little to the forage value of the prairies.

Typically, the prairies are summer range. The salt plains, however, are resorted to more in winter than in summer. Probably, as suggested by Raup (1933), the lack of fresh water renders them practically uninhabitable in summer.

Two other important elements of the summer range are marshy lake margins and the sloping sides of sink-holes. The former usually have a zone of sedge near the standing water followed by a zone of grasses extending into the willow borders. The latter tend to have a more herbaceous flora, but with a generous sprinkling of edible grasses and sedges. Both types, though individually of little value, are so abundant and widely distributed through the upland forests that in the aggregate they contribute significantly to the total of available summer forage.

Successional trends of the plant communities have not been studied in detail, but it is obvious to any critical observer that two processes are in operation that will have long-range effects on the bison. The first of these is the steady progression toward a mesophytic white spruce (*Picea glauca*) climax forest. Most of the semi-open prairies in the Pine Lake-Flatgrass Lake sector have been invaded by aspen which, in time, is usually replaced by spruce. In many pure stands of jack pine (*Pinus Banksiana*) also, the only seedlings visible are those of white spruce. This will have the effect of reducing the summer carrying capacity of the Alberta Plateau. Curiously, the Salt Plains prairies seem immune to the process. Whether this is due to their youth, as suggested by Raup (1935), to their halophytic nature, or to some other factor or combination of factors, is not known. Since those prairies serve as the major winter range for the bison that summer on the Alberta Plateau, it is conceivable that in a relatively few years the condition may arise (rare in the wildlife field) wherein summer range, not winter range, will be a limiting factor. That is all the more remarkable at a latitude of 60 degrees north.

More or less balancing the loss of range is the steady acquisition of new range as a result of the silting-in of the immense basin west of Lake Athabasca that is a part of the combined deltas of the Peace and Athabasca Rivers. Each year the mud flats rise imperceptibly out of the shallow lakes, and eventually what was once a bay becomes a lagoon and then a sedge meadow teeming with bison.

In the foreseeable future, the carrying capacity is not likely to change appreciably one way or the other. However, a gradual population shift will likely occur as the forests occupy the prairies north of Peace River and sedge meadows arise from the mud flats of the delta south of the river. Significantly, the delta flats were not included within the original boundaries of the park drawn up in 1922. As previously mentioned, in 1926 a few hundred bison resorted to the delta flats, and the park boundaries were extended to take them in. Repeated aerial counts throughout the course of the present investigation have revealed that between 4,000 and 5,000 bison occupy the delta lowlands the year round.

Reproductive Characteristics

Material for this section comes from notes taken on the reproductive condition of the animals killed at the annual slaughters, held usually in the months of December and January, from 1952 to 1956. During those years about 1,800 bison were slaughtered, of which 840 were mature females. All but 218 were taken at the Hay Camp in the Salt Plains section. The remaining 218 (105 mature cows) were removed from the Lake Claire meadows south of Peace River. Since there were apparent differences in the reproductive rates of the two herds, it has been necessary, on many points, to discuss the two herds separately. Also, a method of aging by dental characters had not been devised when the Lake Claire bison were examined, and no four-year-old class was recognized. That renders comparisons between the two herds difficult.

The following information was recorded for each female examined (1) age, (see Fuller, 1959 for method of age determination); (2) presence of milk in the mammary glands; (3) presence or absence of a foetus; (4) size of foetus; (5) sex of foetus; (6) condition of the ovaries. The data are summarized in Tables 6 and 7 for Hay Camp and Lake Claire respectively.

Number of Young at a Birth

No twin foetuses were discovered in any of the 481 gravid uteri examined. Other observers of both American and European bison have generally agreed that twins are rare in this genus.

Primary Sex Ratio

The sex was recorded for 472 of the 481 foetuses examined. There was a slight preponderance of males in the sample—53 per cent or 112 males per 100 females. Palmer (1916) reported a primary ratio of 54 per cent males (119:100 females) in a sample of 460 plains bison.

Duration of the Breeding Season

Mating activity begins in July and the peak of the rut is reached between August 10 and 20. Occasional copulations, or attempts at copulation, are seen throughout the autumn months. Mounting has been observed in the holding corral in December and even early January, but that is not entirely natural. According to Soper (1941), new-born calves have been seen in every month of the year, implying that conception may also take place in any month. In the writer's experience, new-born calves are rarely seen after August, which indicates few conceptions later than November. What appeared to be normal copulation was observed in the field on November 13, 1950. The duration of the breeding season is therefore approximately four months. Within that season the cows are probably polyoestrous, with a cycle length of about three weeks, unless they differ markedly from the captive bison studied by Heape (1901 *in* Asdell, 1946).

Age of Females at First Conception

The female bison examined did not all attain sexual maturity at the same age. At Hay Camp about one-third (38 per cent) of two-year-old cows and 65 per cent of three-year-old cows examined were pregnant (Table 6). However,

Table 6. Reproductive statistics of female bison in the Hay Camp herds, Wood Buffalo National Park, 1952-53 to 1955-56

Age at death	2 yrs	3 yrs	4 yrs	Young adult	Adult	Aged	Entire sample
Number in sample	160	92	120	95	192	74	733
	%	%	%	%	%	%	%
Reproductive condition							
Pregnant only	36	52	37	40	28	8	34
Lactating only	2	27	20	27	27	34	21
Pregnant and lactating	2	13	26	26	30	18	19
Total breeding*	39	92	83	94	84	59	74
Large Corpus luteum; no visible foetus	0	3	5	3	3	7	3

*Apparent errors in totals are due to rounding.

since 13 per cent of the three-year-olds were also lactating, they had initially conceived as two-year-olds, thus leaving 52 per cent which conceived for the first

time as three-year-olds. That leaves a residue of 12 per cent which either breed as four-year-olds (or older) or are sterile. A similar figure can be arrived at in another way by considering the 1950 and 1951 year classes. Some of the females born in 1950 were examined in 1952-53 as two-year-olds, and others in 1953-54 as three-year-olds. The observed conception rates were 39 per cent and 50 per cent respectively, leaving 11 per cent unaccounted for. Cows born in 1951 showed a conception rate of 48 per cent as two-year-olds (examined in 1953-54) and 43 per cent as three-year-olds, (examined in 1954-55), leaving 9 per cent to mature at a more advanced age or remain sterile.

There is a suggestion of earlier maturation in the Lake Claire herds. Fifty-nine per cent of the two-year-olds and 81 per cent of the three-year-olds examined in 1952 were pregnant (Table 7).

Table 7. Reproductive statistics of female bison in the Lake Claire herds, Wood Buffalo National Park, January 1952

Age at death	2 yrs	3 yrs	Young adult	Adult	Aged	Entire sample
Number in sample	17	31	42	9	6	105
	%	%	%	%	%	%
Reproductive condition						
Pregnant only	59	52	57	33	33	52
Lactating only	12	3	10	22	0	9
Pregnant and lactating	0	29	29	44	0	24
Total breeding*	71	84	95	100	33	85

*Apparent errors in totals are due to rounding.

A few precocious females conceive as yearlings. At Lake Claire, in 1952, one of 11 yearlings examined contained a small foetus. Additional evidence is supplied by the finding of eight lactating two-year-olds which must, therefore, have conceived as yearlings. At Hay Camp, six of 160 two-year-olds examined were lactating, while at Lake Claire there were two lactating two-year-olds out of 17 examined. Those proportions are small enough that they do not materially affect the productivity of the herd.

Both Hornaday (1889) and Seton (1929) state that female bison begin to breed "at three years", but both fail to define "breeding". If the term is used in the sense of bearing a calf, then it implies taking part in the rut at two years of age. It is doubtful that this is the meaning those authors intended. The breeding season among mammals is usually thought of as the period of the rut. Hornaday

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and Seton undoubtedly were unaware that at least some bison cows conceive as two-year-olds. Leopold (MS 1925) states that on the Wichita Reserve, bison cows regularly have calves at three years, occasionally at two. Negus (1950) records calf production by four of seven three-year-olds at the Wildlife Park, Moran, Wyoming. That small sample gives a conception rate among two-year-olds about equivalent to that of the Lake Claire herds. Zabinski (1949) presented detailed individual records on 22 wisent cows, 16 of which produced their first calf at or near the fourth anniversary of their own birth. Five others failed to calve until their fifth or sixth year, whereas the remaining one conceived as a two-year-old and produced a calf at 38 months.

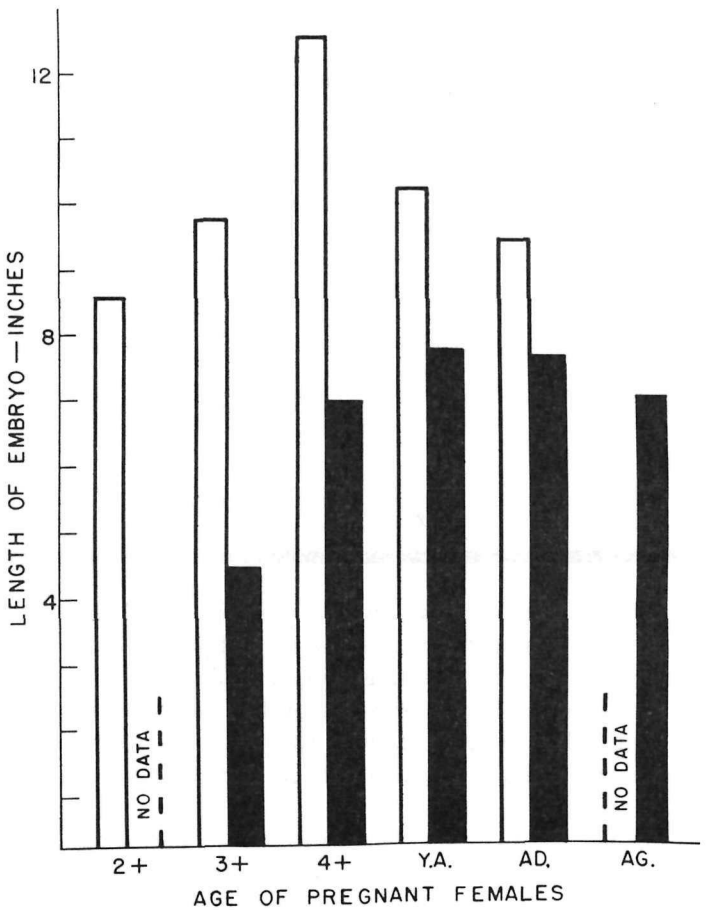

FIGURE 1. Comparison of the length of embryos found in lactating cows (solid bars) and non-lactating cows (open bars) examined during the slaughter of January, 1955.

Influence of Lactation on Subsequent Conception

During each slaughter it was noticed that there was a tendency for cows that were lactating to have smaller embryos than those not lactating. That is illustrated graphically in Figure 1 for 139 cows examined in January, 1955—66 pregnant only and 73 pregnant and lactating. Subjected to Student's "t" test for significance, for three- and four-year-olds, the differences are highly significant ($P=<0.01$); and for the adults the difference is significant ($P=<0.05$). When the data for these four age groups are pooled, the difference is highly significant ($t=5.055$ for 137 degrees of freedom). The simplest explanation is that lactating cows conceive later than non-lactating ones.

Rush (1932) found a variation in embryo size in bison examined at Yellowstone National Park. He took that as evidence of a long breeding season, but attributed it "to the fact that this herd has been artificially fed for the past 25 years, thus lessening the dependence upon favourable seasonal conditions for birth of the young." That explanation cannot apply in Wood Buffalo Park and may not have been valid in Yellowstone.

Frequency of Conception

The conception rate for each age group at Hay Camp is shown in Figure 2.

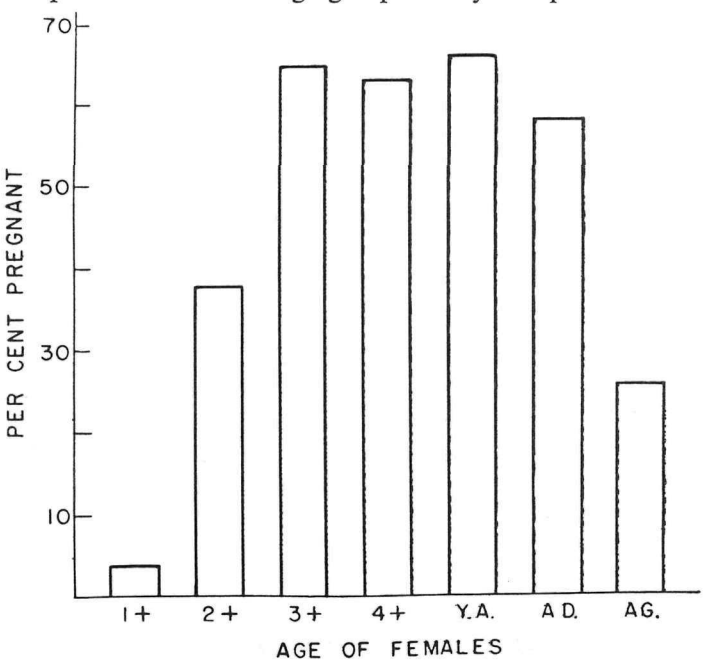

FIGURE 2. Relationship between age and conception rate in 733 bison cows examined at Hay Camp in Wood Buffalo Park, 1952-56.

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The period of greatest reproductive vigour is obviously from three years to the onset of old age (12 to 15 years). During that period each cow must conceive, on the average, about two years in every three to produce the observed average conception rate of 67 per cent. The following general scheme explains most of the field observations. Beginning with a virgin cow, breeding most likely occurs during the peak of the rut in August, and calving the following May. The cow, which is then lactating, seems less likely to be bred in August, but has a good chance of conceiving at some later heat period. If examined during the winter, the cow would be recorded as pregnant and lactating, with a smaller than normal foetus. That calf would be born in late spring or early summer, probably precluding August breeding altogether and greatly reducing the cow's chance of conceiving during a later oestrus cycle. The following summer, since no calf would be produced, the cow would be ready to breed again in the main August rut.

One variable that might materially alter the scheme would be the fate of the calf. Survival of the calf apparently reduces the female's chance of conceiving again. Early death of the calf, on the other hand, probably removes that restriction. There is thus evidence of an autoregulating or compensating mechanism.

Influence of Tuberculosis on Conception Rate

A priori, it might be expected that tubercular females would produce fewer offspring than healthy ones. Contrary to expectation, tubercular cows have shown just as high a conception rate as healthy ones. At Hay Camp 55 per cent of 323 tubercular cows and 51 per cent of 331 healthy cows were pregnant. At Lake Claire the figures were 81 per cent of 26 tubercular cows and 66 per cent of 95 healthy cows. Because neither of those differences is significant statistically, there is at present no evidence that tuberculosis has any effect on the conception rate.

Comparison with Other Herds of Bison

Only one published account of the incidence of pregnancy in a herd of bison was found (Rush, 1932). In addition, Banfield's (1952) unpublished report of an investigation of bison in Elk Island National Park, Alberta, was available, and a letter (June 7, 1951) from Richard E. Griffith, Chief of the Section of Habitat Improvement, Branch of Wildlife Research, U.S. Fish and Wildlife Service, which contains similar information for the National Bison Range, Montana. These data are included in Table 8.

The Hay Camp herds have a conception rate about equal to that at Yellowstone (Rush, 1932), where Bang's disease (brucellosis) is known to be present. After several unsuccessful attempts to get blood samples to the laboratory, Bang's disease was confirmed in Wood Buffalo Park bison in January, 1956. The incidence of the disease approaches 50 per cent in the Lake Claire herd and probably is of

comparable incidence in the Hay Camp animals. Its presence may help to explain the low conception rate in the Hay Camp herd. Other contributing factors may be the more rigorous climate, and the larger proportion of aged animals in Wood Buffalo Park as compared with Elk Island National Park, for example, where the five- and six-year-olds are culled in the biennial slaughters.

Table 8. Conception rate in four herds of bison

NOTE—Information from Yellowstone Park from Rush (1932); Elk Island National Park from Banfield (*MS* 1952); National Bison Range from Griffith (letter of 7 June, 1951).

Locality	Age of females				Entire sample
	2-3 yrs	4-14 yrs*	15-30 yrs	Unknown	
Lake Claire					
No. in sample	48	51	6	0	105
Per cent pregnant	73	84	33	—	76
Hay Camp					
No. in sample	252	407	74	0	733
Per cent pregnant	48	67	27	—	57
Yellowstone					
No. in sample	—	—	—	184	184
Per cent pregnant	—	—	—	65	65
Elk Island					
No. in sample	1	254	0	0	255
Per cent pregnant	100	85	—	—	85
National Bison Range					
No. in sample	—	—	—	—	64
Per cent pregnant	100	88	74	—	86

*Four years through adult age classes in Wood Buffalo Park equivalent to this category.

Sexual Maturity in Males

During the present study, a portion of the testis and epididymis from each of 20 young males was preserved and examined microscopically for the presence of sperm. The results were as follows: 1 of 6 yearlings, 3 of 8 two-year-olds, and 6 of 6 three-year-olds had abundant, apparently normal sperm in the cauda epididymides. The age of sexual maturity in males, therefore, appears to be essentially the same as in females. A small proportion of males attains sexual maturity as yearlings; a third or more mature as two-year-olds; and probably all three-year-olds and older are mature.

Calf Ratios and Recruitment

In this section it is again necessary to treat different areas of the park separately. The central part of the park was studied mainly from the ground, whereas

the Lake Claire herds were observed from the air. The road from Fort Smith to Pine Lake intersects the summer range of those bison that winter along the Slave River. Thus, at least a part of the population studied in summer was sampled in the winter slaughters at Hay Camp.

The difficulties of securing a calf count varied with the method employed. Aerial counts required speed in segregating calves from older animals. Until August, when the calves begin to lose their reddish coat, this is quite a simple matter. When they acquire their dark winter coat, size is the only differentiating character, and the segregation is slower and more difficult. Two observers were usually employed—one to record all animals, including calves, and one, the writer, to record calves only. Thus, only one person differentiated calves throughout the study, so that identification error was kept constant. Most ground counts were made along the roads, which are merely long narrow gashes through the forest. The animals had to be recorded before they disappeared into the trees on either side of the road. Under those conditions, it was often difficult to get a complete count on a herd. Calves, especially, might pass unnoticed behind or beneath other animals. Such counts are therefore thought to be conservative.

Aerial Counts (Lake Claire).—The most complete record of seasonal variation in calf ratios was obtained in 1951. The results of seven aerial counts in the Lake Claire area in 1951 are shown in Table 9. Spot checks for comparative

Table 9. Results of seven aerial calf counts over the Lake Claire Meadows in 1951

Date	No. in sample	Per cent calves	95 per cent * confidence limits
May 16	675	10	7.9-12.5
June 5	766	18	16.2-21.2
18	1,211	16	14.0-18.2
July 9	903	23	20.3-25.8
22	727	17	14.3-20.0
Sept. 24	376	19	14.2-23.4
Dec. 6	181	12	7.7-17.6

*Estimated from Table II in: Mainland (1948).

purposes were made in the later years. In 1951 calving was obviously incomplete on May 16 and probably also on June 5. The peak was observed on July 9 with a ratio of 23 per cent calves. This was followed by a decline to 19 per cent in September and 12 per cent in December. The observed values on June 18 and July 22 are too low to fit in their proper places. The probable reason is that on both days, the animals were found in large herds of 100 to 250, whereas on the

other counts, the herds were split up into smaller groups of 40 to 80. The chance of missing some of the calves is greater in the larger herds.

Two counts in 1952 yielded calf ratios of 12 and 14 per cent in July and August, respectively. No reason can be advanced for the low counts in 1952 except that it may have been a poor calf year on the Lake Claire meadows. The low results were unexpected, since the incidence of pregnancy there was high, according to the sample studied in January and February, 1952 (see above). However, a good deal of wolf activity was noted in the area in the spring of 1952, so that calf mortality may have been exceptionally high that year. Identical calf ratios of 21 per cent were obtained on July 30, 1953 and August 5, 1954. Those counts are quite in line with expectations.

A potential calf crop is indicated of 20 to 25 per cent in late June and early July, subject to a decline of about 2 per cent per month until December. Less than one-half of the calves born, therefore, survive to the beginning of the new calendar year.

Ground Counts (Park Trails).—The ground counts are summarized in Table 10. The proportion of calves in the herds of the central part of the park

Table 10. Calf counts on Park trails, by months, 1950-53

Year	Month			
	June	July	August	Sept.
1950				
Number segregated	0	0	1,065	497
Per cent calves	—	—	12	10
1951				
Number segregated	430	0	321	0
Per cent calves	14	—	16	—
1952				
Number segregated	0	247	188	0
Per cent calves	—	23	18	—
1953				
Number segregated	0	378	211	0
Per cent calves	—	17	14	—
1950-53				
Number segregated	430	625	1,785	497
Per cent calves	14	19	14	10

tends to be lower than in the Lake Claire herds. That is to be expected in view of the apparently lower fertility of those herds as disclosed at the Hay Camp slaughters. The single exception came in 1952 when, as noted, the Lake Claire herds had an unexpectedly low proportion of calves. In both populations the decline in calf ratio was in the order of 2 per cent per month.

Autumn and winter counts along the trails cannot be made because most of the herds have deserted the accessible areas for the winter ranges, which cannot be penetrated by mechanical transport.

Late-winter Counts (the Park as a Whole).—Late-winter counts were made as part of the aerial strip-censuses of February, 1949 and January, 1951. A third count was made over the Slave River wintering areas in April, 1951. The results of the counts were as follows: February, 1949, 8 per cent calves in a sample of 323; January, 1951, 6 per cent calves in a sample of 324; April, 1951, 6 per cent calves in a sample of 47.

The sample sizes are relatively small, but there is close agreement in all three counts. The data indicate that by the end of their calfhood year, the proportion of surviving calves is down to less than 10 per cent of herd strength from the July maximum of more than 20 per cent.

Yearling and Juvenile Counts.—Herd composition is discussed in detail in another paper (Fuller, 1960). In a pooled sample of 1,465 animals segregated over four summers, yearlings comprised 7.6 per cent, and spike-horns comprised 11.3 per cent. Since some of the 200 unclassified animals were probably either yearlings or spike-horns, the figures could be increased by 2 to 3 per cent. The agreement between late-winter calf ratios (6 to 8 per cent) and summer yearling ratios (7 to 9 per cent) is good.

The spike-horn class consists mainly of two- and three-year-olds. Since those two age-classes combined make up 11 to 15 per cent of total animals, each age must contribute about half. In other words, two-year-olds and three-year-olds each make up about 5 to 8 per cent of the total herd. It is evident, therefore, that a high calfhood mortality rate does not carry over into the older age-classes. Therefore, survival to yearling stage is practically synonymous with recruitment into the breeding population. For management purposes, it is sufficiently accurate to say that recruitment is currently between 5 and 8 per cent per year.

Mortality Factors

Tuberculosis

Tuberculosis is a chronic infectious disease of man and animals caused by *Mycobacterium tuberculosis*—a slender, rod-shaped, acid-fast micro-organism. There are three types of *M. tuberculosis*—human, bovine, and avian. Cross-infection is possible, particularly between the human and bovine types. In general, the organism is sensitive to heat and resistant to cold.

The method of entry of the tubercle bacillus into the animal body and its subsequent dissemination is of some importance when one considers possible means of control. Veterinarians recognize five modes of infection (Thornton, 1949). They are by way of (1) the respiratory system, (2) the alimentary system, (3) the genital system, (4) the skin, and (5) by seepage through the placenta—the congenital form in calves. The first two account for about 95 per cent of the tuberculosis in domestic cattle, and the respiratory route is about ten times as important as the alimentary.

A description of the course of tuberculosis in cattle may be found in any good veterinary text. Greatly simplified, it may be stated as follows: Entry of the bacilli into the animal body gives rise to a primary lesion at the site of infection, which is followed by involvement of the efferent lymph node. The primary lesion may be submicroscopic, whereas lesions in the lymph nodes are easily discovered by slicing the node with a sharp knife. Caseous lesions indicate an active infection, but calcification occurs if the bodily defences of the host succeed in arresting the progress of the infection. Primary infection also gives rise to increased resistance on the part of the host to a second infection.

If the defensive powers of the body are low, the primary lesion may extend through the infected organ and erode into a blood vessel. Other organs may then be invaded metastatically by the haematogenous route. If large numbers of bacilli are involved, the disease enters an early acute stage which is often fatal (acute miliary tuberculosis). If invasion of the blood stream is of a lesser magnitude, the disease becomes chronic, and generalization proceeds slowly. Imposition of a non-specific stress at that time may lead to a breakdown of bodily resistance. Should that occur, the result is acute late generalization which is also fatal.

In congenital tuberculosis, the infection is carried directly to the capillaries of the foetal liver by the umbilical vein, and that organ, rather than the lungs, tends to be the centre of dissemination. Haematogenous spread is common, resulting in early generalization, and, frequently, death.

The Spread of Tuberculosis in Bison.—The post-mortem findings at the 1952 slaughter (chosen because a complete record of the location of tubercular lesions was obtained that year) showed the following distribution of visible tubercular lesions: 34 in the thorax only; 10 in the head and thorax; one in the mesenteric nodes only; and one in the head and mesenterics. Those with lesions in the thorax, or head and thorax (44) were probably infected by the respiratory route, whereas those with lesions in the mesenteric nodes, or head and mesenterics (2) may have acquired the infection by the alimentary route. This suggests a ratio of respiratory to alimentary infections of about 20 to 1, which is higher than is common among cattle. Two females had tubercular metritis. That does not constitute proof of infection via the genital route, but it is likely that those animals would be capable of transmitting the disease by that means.

Congenital tuberculosis does not appear to be common in bison. In the first place, the cow must have tuberculosis of the uterus, which is usually associated with late stages of generalization. Probably the disease is not so far advanced in more than 1 or 2 per cent of the cows giving birth to calves. In the second place, tubercular metritis does not invariably result in a congenital infection of the calf. In the third place, the disease is not always fatal. It seems quite safe to assume, therefore, that calfhood mortality from congenital tuberculosis is low.

Thus, it is presumed that tuberculosis spreads through a herd of bison chiefly by the respiratory route. The gregarious habits of the species undoubtedly are essential in the maintenance of the disease in that way. That type of dissemination does not seem amenable to control.

Incidence of Tuberculosis by Age and Sex.—The incidence of tuberculosis by age and sex in the Hay Camp herd is shown in Table 11. The Lake Claire herd is omitted from the present discussion because the sample examined was small.

As expected, the incidence increases with the age of the animals. The increase seems to be continuous among males, whereas it appears to level off and fluctuate between 50 and 60 per cent among females. But because the observed differences between the incidence in males and that in females are not significant statistically, the sexes have been combined in the last two columns of the table.

Acquisition of tuberculosis appears to be a function of age (length of exposure) up until the third or fourth year. Just why the incidence should level off after that is puzzling, but two possibilities suggest themselves. First, the disease terminates fatally in a proportion of cases (see p. 29) and thus, infected animals

Table 11. Incidence of tuberculosis by age and sex among 1,508 bison examined at Hay Camp, 1952-56

Age	Males		Females		Both sexes	
	examined	% T.B.	examined	% T.B.	examined	% T.B.
Calf	75	23	91	9	166	15
Yearling	138	29	140	37	278	34
2 years	177	38	161	32	338	35
3 years	64	47	93	47	157	47
4 years	25	48	123	48	148	48
Yg. adult	23	74	97	50	120	54
Adult	21	71	199	51	220	53
Aged	4	25	77	57	81	56
All ages	527	38	981	41	1,508	40

are being removed from the population. Second, it is possible that animals that have not become infected by their third or fourth year are genetically more resistant to tuberculosis.

Mortality Caused by Tuberculosis.—Since tuberculosis may affect the host animal in so many different ways, it is difficult to determine how much mortality it causes. A minimum infection, consisting of a microscopic primary lesion and involvement of the regional lymph node, can hardly influence the survival of the affected individual. On the other hand, late generalization, with involvement of several vital organs, must severely handicap it. Just where the line should be drawn between no effect and some effect is a difficult question. Similarly, it is difficult to decide what proportion of the cases terminate fatally.

The criterion adopted in this report is the suitability of the carcass for human food. A totally condemned carcass is considered to have been close to death from tuberculosis. Justification is found in the reasoning used by the meat inspectors in their code of judgment. Tubercle bacilli can only survive in muscle for a short time (7 to 9 days according to Thornton, 1949). Therefore, the meat is considered safe for human consumption unless there is evidence of continual reinfection of the muscles through the blood supply—that is, if there is massive haematogenous dissemination. When the disease has advanced to that stage, it is generally conceded that the bodily defences are incapable of coping with it and the prognosis is negative. Because of the many variables involved, the decision as to when a carcass should be condemned cannot be wholly objective, but the subjective element is certainly minimal.

Table 12 was prepared to show the numbers of totally condemned animals in four slaughters at Hay Camp. The four-year combined average was 5.0 per cent. Some of the variability from year to year may be attributable to the subjective element. The same veterinarian was present in 1952 and 1954, and his results are consistent. Two different inspectors, both of whom judged more severely than the first man, were present in 1955. The 1956 figure was unexpectedly low, but probably indicates chance variation. The cautious attitude of the inspectors in 1955 raises the four-year average considerably, so that 5.0 per cent is considered to be a liberal estimate of the mortality from tuberculosis.

Table 12. Proportion of totally condemned carcasses in four slaughters at the Hay Camp

Year	No. examined	No. condemned	Per cent condemned
1952	245	9	4
1954	276	9	3
1955	782	54	7
1956	205	3	1
1952-56	*1,508*	*75*	*5*

At Lake Claire, where the incidence of tuberculosis was generally lower, the proportion of total condemnations was about the same—eight in a sample of 218, or about 4 per cent.

The distribution by sexes of the estimated mortality is also interesting. Fifty-nine of the total condemnations were females, and only 13 were males. The ratio differs significantly from unity (chi-square = 7.83), suggesting a real difference in the severity of tuberculosis in the two sexes. In searching for an explanation of this observation, it seemed that the stress of pregnancies might make the females more susceptible to tuberculosis. That hypothesis finds support in some work reported in the medical literature. For example, Laurie *et al.* (1951) reported that "the periodic exposure of resistant rabbits to chorionic gonadotropin enhances their susceptibility to the disease" (tuberculosis). Selye (1955), in a review paper on stress and disease, states "It is perhaps not too far-fetched to consider the possibility that an increased ACTH and cortisol secretion during stress may play an important part in the development of clinical tuberculosis". And again "It is a well known fact that in patients suffering from tuberculosis the disease is especially readily aggravated by exposure to any kind of stress situation". Pregnancy has, therefore, two effects. First, the production of chorionic gonadotropin and second,

the imposition of stress, both of which are suspected of enhancing the susceptibility of man and some experimental animals to tuberculosis.

Most advanced cases seen are the results of long-standing or chronic infection. Complete figures for the age distribution of condemned carcasses are lacking, but the 9 condemnations for 1952 were distributed as follows: two-year-olds—1; four-year-olds—1; young adults—1; adults—1; aged—5.

Early acute generalization seems to be rare. For example, in 1952 only one case of acute miliary tuberculosis was recognized, as compared with eight chronic generalizations. The acute form is the more rapidly fatal; therefore, there is less chance of encountering animals in that stage of the disease during the short period of the slaughter. The mortality rate has to be revised upward slightly to take account of that. Adult mortality from tuberculosis, therefore, probably runs between 4 and 6 per cent of total animals.

Origin of Tuberculosis in Wood Buffalo Park.—Two lines of evidence suggest that tuberculosis was introduced with the plains bison from Wainwright. First, tuberculosis was known to be present in a high proportion of the Wainwright bison before 1925 (Cameron, 1923, 1924; Hadwen, 1942). None of them was tested before shipment, but it is inconceivable that 6,600 could have been drawn from a heavily infected population without including diseased animals. Second, the incidence of tuberculosis decreases as the distance from the site of introduction of the Wainwright animals increases. Thus, at Hay Camp, the release site, the incidence was 46 per cent in 1952 ($N = 245$); on the Salt Plains west of Fort Smith about 40 miles from the release site, it was 29 per cent in 1950 ($N = 79$); while at Lake Claire, at a distance of about 60 miles, it was 20 per cent in 1952 ($N = 218$). The incidence in the sample from the Hay Camp differs significantly from that at both Lake Claire and the Salt Plains, thus suggesting that there is a real difference in the populations from the three areas. It is recognized that other factors may influence the incidence of tuberculosis in different regions, but the distribution is typical of what one would expect to find if a disease (or other characteristic) spreads from a central focus.

Other Diseases

Brucellosis—The low incidence of pregnancy at mid term in the Hay Camp herd suggested the presence of brucellosis (*Brucellosis abortus*) as a contributory factor. Blood samples for agglutination tests were taken during the slaughters of 1952-53 and 1953-54, but no results were obtained because the samples either froze or haemolysed during collection or shipment. In 1956, 12 specimens were collected, and the serum carefully transferred to sterile vials for shipment. Eleven of them arrived at the laboratory in a condition satisfactory for testing, and three proved positive. Subsequent investigations at Lake Claire in 1957 revealed that 69 of 200 animals (35 per cent) tested by a veterinarian of the Department of

Agriculture gave a positive titre for brucellosis. Incidence for 1958 was 45 per cent (228 of 640 animals tested). Those findings open a field of investigation beyond the scope of the present study.

Arthritis—Arthritis has been recorded in about 2 per cent of the carcasses examined during slaughters. It is found oftenest in mature and aged animals, but one yearling and one two-year-old have been recorded as infected. The stifle is the joint most commonly attacked. In some animals the arthritic joint is also tubercular, in which event it is difficult or impossible to decide which condition came first. Arthritis also is known to be associated with brucellosis in cattle. Hadwen (1942) recorded arthritis in Wainwright buffalo.

Severe arthritis, involving more than one limb, is seldom seen. The probable reason is that the crippling effect of the disease makes the afflicted animal easy prey for wolves (*Canis lupus*), so that the cripples are weeded out before the disease progresses far.

Arteriosclerosis—Thin, brittle, calcareous plates have been found on the inner wall of the aortic arch and posterior aorta. That condition probably represents an incipient arteriosclerosis. No estimate of the frequency of the condition can be made because the aorta was not routinely examined. Cameron (1923) recorded a similar condition at Wainwright Park.

Miscellaneous Diseases—A number of other disease conditions, all apparently rare, and several unidentified, have been discovered. Because of their rarity, they have little significance as population controls. There were seven cases of orchitis of unknown origin. That condition will require more attention in the future because abscesses of the testes are typical of brucellosis. Non-tubercular chronic orchitis was recorded by Hadwen (1942) in bison from Wainwright, Alberta. Another testicular lesion was diagnosed as a malignant lymphosarcoma by the Veterinary Pathologist, Alberta Department of Agriculture. Cameron (1923) discovered two such tumours in bison he examined at Wainwright. Four cases of an unidentified (but non-tubercular) infection of the uterus and foetus have been noted. The foetal membranes did not show the leathery appearance typical of brucellosis. Abscesses of unknown origin have been found in the hip, shoulder, and stifle. They are thought to have resulted from local infection in each case. Non-tubercular abscesses of the liver have also been noted. One case of pneumonia and one occurrence of renal calculi were discovered during the 1952 slaughter.

Anatomic Anomalies

Two anomalies have been noted, neither of which has any known pathological significance. One animal examined in 1952 had a melanotic spine, and about 1 per cent of all the specimens were found to have a bifurcated gall bladder. Cameron (1923) found the latter condition in 7 per cent of the animals he examined at Wainwright.

External Parasites

Damalinia (Bovicola) sedecimdecembrii—This louse was recovered from one aged female in the spring of 1955. The infestation was severe and had resulted in the loss of most of the hair. Mange was suspected, but skin scrapings revealed no mange mites. Adult lice were much in evidence on the hairs. This is the only external parasite recovered from the bison in the park. The specimens were identified by G. H. E. Hopkins of the Zoological Museum, Tring, England.

Internal Parasites

Setaria labiato-papillosa—Specimens of this worm were identified by Dr. T. W. M. Cameron of the Institute of Parasitology, MacDonald College. Since it is non-pathogenic, definite records of its occurrence were not maintained. However, it probably infects 5 to 10 per cent of the bison. Cameron (1923) found this worm in "many" buffalo at Wainwright.

Dictyocaulus—Lungworms were observed in three bison carcasses. Specimens from one of these were preserved, but were lost subsequently. They were thought to belong to the genus *Dictyocaulus,* the thread lungworm.

Discussion of the Effects of Pathogens

Because of the excellent facilities for post-mortem inspection available, and the large sample of bison examined, the above list of abnormal and pathological conditions is reasonably complete. One or two features of the list require additional comment.

Very few of the conditions discovered appear serious enough to be the direct cause of the death of the host. A few (arthritis, lungworm) could be predisposing factors to death by predation or otherwise place the animal at a disadvantage (depilation by *Damalinia* in winter). The majority of the conditions appear to have little influence on the well-being of the host. Secondly, with the exception of arthritis and *Setaria,* none has been encountered in more than 1 per cent of the animals examined. The mortality resulting directly or indirectly from those conditions must therefore be very small. The effect of brucellosis is being given additional study.

Of perhaps equal interest are the parasites that have not been found in Wood Buffalo Park bison, although they were present in the transplanted Wainwright animals. Cameron (1923, 1924) recorded *Sarcocystis* "in many hearts", *Hypoderma* larvae in "practically all the buffalo", and *Fascioloides magna* in several livers. Every heart and liver was inspected in the current study before being passed as human food, so it is virtually impossible that either *Sarococystis* or *Fascioloides* is now present in Wood Buffalo Park. Similarly, *Hypoderma* larvae in the hides could not escape detection. Something in the northern environment may prevent those forms from completing their life cycles.

Another significant omission is the hydatid worm, *Echinococcus granulosus.* Cameron (1923) recorded one doubtful liver cyst, and one was observed in 1954. Dogs, wolves, caribou (*Rangifer arcticus*), and probably foxes (*Vulpes fulva*) and moose (*Alces americana*) carry that worm in the park or its environs; therefore the bison must be exposed. Bovids are known to be more resistant to the parasite than cervids. That may be the explanation of its absence in bison.

Other parasites that have not been found in Wood Buffalo Park are stomach worms *Haemonchus, Esophagostomum,* and *Cooperia,* all recorded by Cameron (1923, 1924). That may have been because the stomach was not included in routine post-mortem examination at the annual slaughters.

Predation

The only animal for which there is direct evidence of predation on bison is the timber wolf, *Canis lupus.* This section is, therefore, concerned only with predation by wolves.

In 1951 a study of the wolf was initiated on a small area readily accessible from Fort Smith. Much information has accumulated since that time, not all of it pertinent to the present study. Results of the first year of the program have been published by Fuller and Novakowski (1955). The plan and operation of the project subsequently have been kept constant from year to year. It is hoped that the project will be continued for a longer period. Any conclusions stated at this time must be considered tentative.

Food of Wolves—The results of the examination of 95 wolf stomachs are shown in Table 13. It is difficult to evaluate the results when so many of the

Table 13. Food items found in 95 wolf stomachs taken on the winter range of the bison in three successive winters

Year	Bait only	Bison remains	Other	Total
1951-52	8	35	6	49
1952-53	27	4	5	36
1953-54	1	0	9	10
Total	36	39	20	95

stomachs (36) contained bait only. If those 36 specimens are excluded, bison formed about 65 per cent of the food of the remaining 59. That is still misleading, because nine specimens taken at the same bait on the same night in 1954-55 were obviously all members of one pack and all had moose hair in their intestinal tracts. That single occurrence biases the results unduly in such a small sample.

Whenever wolf scats were found, they were collected and examined. Most were recovered in summer, whereas the stomach analyses refer to early winter. Of 63 scats examined, 54 (86 per cent) contained bison material. The two independent lines of evidence indicate that bison forms the staple diet of the park wolves.

Examination of Wolf Kills—Eleven case histories representing wolf kills are discussed in this section. That may seem a small number, but its smallness is partly offset by the completeness of the information. Finding a wolf kill at all in that large area with so few trails is a matter of chance. It is remarkable that three wolf attacks were actually interrupted, and on two other occasions the carcasses of the victims were still warm when found. In addition, two of the victims were almost certainly seen alive within 48 hours before death.

(1) On November 16, 1950, during a small local slaughtering operation, the tracks of two calves and six wolves were observed within half a mile of camp. Since hunting had been going on for two weeks, and 73 buffalo had been killed, many of them cows, it is likely that the calves were orphans. After the party followed the tracks for about eight miles and emerged on a large prairie, they saw the wolves attacking a calf. Another calf was standing about 30 feet to one side, apparently unconcerned. On our approach the wolves took flight. This second calf was shot and proved to have been previously uninjured. The first calf was dead and partly eviscerated. The wolves had attacked its right shoulder, flank, and thigh, but had not hamstrung it. This example showed that wolves do not have an easy time, even with practically defenceless calves five to six months of age. The chase lasted at least eight miles, and an area at least 25 feet in diameter at the site of the final encounter was trampled flat, showing that the calf had put up a battle. It also demonstrated that bison not under actual attack by wolves pay no attention to them, nor do the wolves seem interested in more than one victim at a time.

(2) On June 27, 1951, a herd of buffalo in an agitated state was seen along the Pine Lake road. They entered the woods as the observers approached. Their behaviour was recognized as abnormal and a stop was made just in time to catch a glimpse of two grey wolves. One cow remained behind, and a search of the area disclosed a badly mauled male calf, lying behind a dead tree. An autopsy disclosed fresh wounds on the fore and hind legs and two one-inch gashes in the abdominal wall. The paunch was bruised and the left lung hemorrhaged. There also were gangrenous wounds, several days old, in the large thigh muscles. There was no evidence of tuberculosis. There again was evidence of a difficult time for wolves in securing a calf. The old wounds were proof of an earlier unsuccessful attack on the calf. There was also evidence that the cow stayed by the calf, as she was driven away by our party only with some difficulty.

(3) On October 6, 1952, a local resident was returning to Fort Smith from the park when he interrupted a wolf attack and found a male calf nearly dead. He put the calf out of its misery and delivered it to the writer. On autopsy it, too, showed fresh wounds (the right thigh was about half gone) and wounds on the fore quarters several days old and gangrenous.

(4) A very old male with horns worn to blunt stubs was discovered dead and mostly eaten on October 22, 1951. The few remains were frozen too hard to permit a search for tuberculosis. From the condition of the horns and teeth, there was no doubt of the extreme age of that individual.

(5) On November 4, 1951, N. S. Novakowski, who was employed on the wolf project, discovered the carcass of an aged female bison, frozen and partly destroyed. That animal had been seen alive on November 3, when it had blood on one flank, and part of the tail was missing, presumably as the result of a wolf attack. The missing tail served for identification in that case. Tuberculosis was not found in the remains, but the autopsy was incomplete. Again, an unsuccessful first attack was indicated by the evidence.

(6) The carcass of an aged female that had obviously been downed by wolves was found by Novakowski on March 3, 1953. Examination of the head glands showed no evidence of tuberculosis. The remainder of the carcass was unfit for autopsy. Strychnine was placed in the carcass on March 4, and three dead wolves were found nearby on March 5. A herd of 14 bison, with two calves, was grazing about 100 yards from the carcass and the dead wolves on March 5.

(7) On August 20, 1952, the scattered remains of a very old bull were found near a small sink-hole pond just off the Peace Point-Pine Lake road. An old weakened bull, presumably the same one, had been observed there frequently throughout the summer. He had refused to leave even when a road construction crew camped by the waterhole for several days. The waterhole was in a grassy opening surrounded by a pine forest, so that it supplied all his requirements of water, food, and shelter. Old bulls often spend their last days in similar situations, and their skeletons are frequently found nearby.

(8) On October 7, 1954, the carcass of an aged male was found at the old Mission Farm, southwest of Fort Smith. There was little evidence to link wolves with the actual killing of that animal, but judging by the horns and teeth, it was the oldest animal seen during the course of the investigation.

(9) An adult male was autopsied on July 6, 1951. That animal had been seen alive the previous day when it appeared too weak to rise to its feet as a vehicle passed nearby. It had probably been dead less than 24 hours when examined, but most of the abdominal viscera had been removed by wolves. The autopsy showed retropharyngeal glands with tubercular lesions larger than oranges, lung lesions, and "grapes" on the pleura, sufficient evidence on which to base a diagnosis of advanced generalized tuberculosis. That animal must have been a menace to any

that came in contact with it. The wolves had actually performed a service in herd sanitation when they ended its career.

(10) On August 23, 1951, four bison, two bulls and two cows, appeared on the road and approached to within 150 feet of the writer's parked truck. In a few minutes the first of 11 wolves appeared, and one cow was noticed that had wounds on the thighs and around the anal and genital openings. After more than an hour of watching, the wolves left the scene and the injured cow was collected. It proved to be a two-year-old with a small lesion, probably tubercular, in the bronchial lymph node. It also had an infected wound in the right hip, the anterior tip of the ilium shattered by a bullet, and a severe peritonitis. It was quite clear that the cow had been singled out by the wolves because it was already crippled by the bullet wound.

(11) On November 16, 1951, Novakowski and a guide, while servicing wolf-bait stations, found a wolf-killed young adult female that was still warm. The writer performed an autopsy the following day and found (1) a tubercular lesion in the anterior mediastinal node and (2) a broken right fore leg. The tuberculosis was insufficient to handicap that individual. It was not determined whether the leg was broken before or during the wolf attack.

Discussion—Very old animals are generally considered to be a biological surplus, and the loss of individuals in that class to predators or from any other cause is not usually detrimental to the general herd welfare. In five of the 11 case histories presented, the victims belonged to that class. There is no evidence that such "normal" predation is detrimental to the bison. The aged class provides an indicator to the situation. In a long-lived species such as the bison, the aged class must be replaced slowly, and it appears evident that excessive predation would remove individuals from that class faster than they could be replaced. Therefore, the very presence of a substantial number of aged animals in the population is in itself evidence that the predation is not unduly severe. The calf class, too, contains a large surplus element. Only a small annual increment is required to maintain the herd at its present numbers. More calves are produced than are required to satisfy that requirement. Predation on the surplus of calves must also be considered normal and without detriment to general herd welfare.

The third class of animals subject to wolf predation might be called "the handicapped". In our survey it included one animal in the terminal stage of tuberculosis, one with an infected bullet wound, and possibly one with a broken leg. Those animals were all in the productive segment of the population. The evidence so far accumulated shows that segment normally to be immune to wolf predation in the absence of some predisposing factor such as disease or crippling.

Several other points illustrated in the case histories described may bear repetition. First, the wolves are not able to kill buffalo at will. Even calves are not

taken easily, and one aged female apparently beat off a first attack before falling victim to a second. Second, wolves usually, if not invariably, return to their kills. That is demonstrated by case number 6 and other evidence presented by Fuller and Novakowski (1955). Third, the writer has not yet seen an example of a bison being hamstrung; rather, the favourite points of attack are the thighs, shoulders, and flanks.

In summary it may be said that there is so far no evidence that wolves are preying significantly on any but surplus and handicapped bison. It follows, therefore, that predation at its present level is not detrimental to the general herd welfare.

Accidents

Drowning—Drowning was formerly an important factor in the survival of the plains bison (for a review of evidence see Roe, (1951), Chapter VII). It is not surprising, therefore, that drownings should be recorded every year in Wood Buffalo Park. Most of the drowned animals are found in the late spring, leading to the conclusion that they venture out on rotten ice and are trapped when they fall through. Most of the drowning occurs in the Peace River, and affects animals whose spring and autumn migrations take them across that stream. In those seasons human travel in the park is nearly impossible, so that reports from trappers and wardens living along the Peace River must be relied on. The average spring breakup produces reliable reports of probably 20 to 50 bison drowned. Smaller streams also take a toll; for example, a post-partum cow was found drowned in Salt River in early May, 1951.

Some drownings occur in early winter. In December, 1947, four bison were found frozen into the ice of Murdock Creek. The signs showed unmistakably that a considerable herd had ventured on the ice and most had escaped up the bank. Slabs of ice less than two inches thick were thrown up by the victims in their struggles, showing the thinness of the ice when the animals broke through.

Soper (1941) thought most of the drownings were caused by high water during the spring floods, rather than by falling through rotten ice. The writer's estimate of mortality agreed with his (40 to 50 animals per year). Recent events have shown drownings to be much more cataclysmic than previously had been supposed. High water during the spring of 1958 in the Athabasca-Peace River delta killed nearly 500 animals; and severe flooding of the whole shoreline of Lake Claire during the autumn and winter of 1960 may have caused the death of as many as 3,000 animals.

Other Accidents—Soper (1941) mentions such things as miring in bogs or becoming trapped in sink-holes, but dismisses them as insignificant causes of mortality. Since Soper's day a new hazard has appeared—the motor vehicle. The

first, and so far only victim of the machine age was a bull that lost an encounter with a truck on the night of August 27, 1951. The driver's account of the incident is not very clear, but it seems that he failed to see the animal by the light of his headlights. The bison sustained a broken neck and the truck a broken radiator.

Catastrophes—Under this heading might be considered forest fires, blizzards, and midwinter thaw followed by deep freeze. Forest fires and blizzards occur almost every year, but there is no record of excessive deaths among bison attributable to those hazards. Starvation caused by a prolonged thaw followed by a severe freeze has rarely been recorded in the park area. As just pointed out, however, drowning due to unusual water conditions can be a most profound mortality factor, capable of surpassing any other cause of death in that area south of the Peace River.

Summary of Factors Controlling Abundance

In the second chapter it was shown that the wood buffalo, after verging upon extinction in 1890, increased in numbers until 1922 when Wood Buffalo Park was established. Shortly after the introduction of plains bison in 1925-28, Soper estimated the combined population to be 10,000 to 12,000. Two recent aerial censuses, in 1949 and 1951, yielded similar estimates of 10,000 to 12,000. Before the introduction, the average annual increment was probably about 7 per cent (Fuller, 1950). Since the introduction, the numbers have apparently been stable.

In this study, a detailed examination of the rates of reproductive gain showed that the calf crop amounts to between 20 and 25 per cent of the total number of animals, but that mortality in the first year reduces the percentage of survivors to less than 10 per cent. As a result of further mortality before sexual maturity, recruitment into the breeding population is between 5 and 8 per cent annually. The gross annual increment at the present time is about equal to the net annual increment during the period of increase in the first quarter of the century. Since it is not realistic to think that there was no mortality during that period, it is apparent that the gross annual increment must have been greater before 1925 than afterward. That could result in one of two ways—either by greater calf production or by higher survival rates to breeding age. There is no available evidence to indicate which factor may have been the more important.

It has been stated in the consideration of mortality factors, that tuberculosis is the greatest single cause of death in the mature age classes. The estimated 4 to 6 per cent annual loss to tuberculosis is almost enough in itself to offset the 7 per cent net annual increment that obtained before the introduction of diseased plains bison. Again, there is no evidence that other forms of mortality were either more or less severe before 1925 than afterward.

Clearly, one reason for the change from a slowly growing population to a stable one was the 4 to 6 per cent additional mortality imposed by tuberculosis, which was presumably introduced at about the time the change occurred. However, it still seems necessary to postulate a small reduction in the rate of recruitment as well. Brucellosis undoubtedly has played its part by lowering the birth rate.

There is another factor that must have had a bearing, although it is difficult to assess its importance. The growing population from 1890 to 1925 must have been essentially a young population. Undoubtedly, there were a few old animals in 1890 when the total numbers of wood buffalo were under 500, but there would be practically no increase in the proportion of aged animals for some 15 to 20 years, when the increasingly large calf crops had advanced through maturity and had reached old age. It has been established that the aged segment of the population has a lower reproductive rate and a higher mortality rate than the mature segment. Therefore, until an aged class became well established, one would expect to find a larger calf crop and lower total mortality, or, a greater net annual increment.

Management Proposals

Aims of Management

Basically, there are three reasons for wishing to manage any wildlife resource. They may be stated as : (a) for its aesthetic and historical values: (b) for its value as a source of human food; and (c) for its value as an object of the chase. To these must be added a fourth aim of management which is specific in its application to the Wood Buffalo Park herd, (d) elimination or control of disease.

Obviously, there is some overlapping of aims in managing the bison herd. For example, the hunter who hunts for sport also expects to use the meat of his quarry, and the person who hunts in season may have a deep feeling for the aesthetic values of wildlife. To some extent, then, it is impossible to keep those aims entirely separate in discussion. The presence of tuberculosis and brucellosis in the herd adds to the complexity, because these diseases have a far-reaching effect on each of the three primary aims of management. For that reason, the disease problem is dealt with first.

The guiding principle in the following discussion of management proposals is the concept of multiple use. The total range occupied by the bison in Wood Buffalo Park and its environs approaches 20,000 square miles. The distribution of the bison within that area is far from uniform. Furthermore, parts of the range are, or soon will be, accessible to tourists and others, while other parts will remain inaccessible for some time. For those reasons, no single management procedure can work for the entire range. In the less accessible areas, and in areas with only small or moderate bison populations, aesthetic values should be the prime consideration. In areas of concentration where herd management is relatively easy and where range deterioration is a threat through over-population, management should take the form of regulated harvests in which the carcasses are processed for human use.

The Elimination or Control of Tuberculosis

Should further steps be taken to control tuberculosis, and if so, should the objective be merely control, or elimination? To answer, it is necessary to go into the adverse effects of the disease more fully.

The effects of tuberculosis on the bison have already been noted. The mortality it causes has been postulated as a major factor is stabilizing what was formerly a slowly increasing population. Is the lack of increase in the herd at the present time regrettable? The answer must be, with some reservations, in the negative. With a population of at least 10,000, there is no imminent threat of extinction. What is now most to be feared is what has frequently happened to ungulate populations in National Parks—over-population with subsequent damage to the range. To have a large, essentially stable population within the carrying capacity of the range is, in many respects, an ideal situation.

Does tuberculosis reduce the aesthetic value of the herd? Several factors must be considered. It has been shown that with the exception of tuberculosis and brucellosis the herd is remarkably free from diseases and parasites. In about three-quarters of the cases, the signs of tuberculosis are inconspicuous, even at post-mortem, and brucellosis likewise is innocuous in its outward manifestations. Advanced tuberculosis results in general emaciation or arthritis in less than 10 per cent of the herd, and much of that is in the old animals, which are not likely to be thrifty anyway. In that respect it is perhaps less objectionable than screw-worm infection in deer, or warbles in caribou, to mention only two examples. The fact is that most wild animal populations are subject to characteristic diseases and parasites, a situation which the general public has a tendency to accept as unavoidable. Perhaps there is a prejudice against tuberculosis because it is well known as a disease of humans and domestic animals, and active control and eradication schemes against it have been undertaken by both government and privately sponsored organizations. If that bias is set aside, there appears to be no reason to consider tuberculosis any worse aesthetically than other wildlife diseases.

Turning to the human health hazard, it is easy to show that it exists more in theory than in fact. Humans can acquire the disease from bison only by close contact with infected bison either living or dead. To suggest that they can come into contact with the living animals closely enough for infection is so ridiculous as to be absurd, and in order to come into contact with a dead bison one must either kill the animal or find it dead. Molesting the animals in a National Park is illegal, and warnings about tuberculosis should deter the curious from examining too closely any dead animals they may chance to discover. In the normal course of events, carcasses are quickly destroyed by scavengers, so that even the possibility of discovery of an infected carcass is remote.

Another possibility to be considered is the infection of other native ungulates, such as the moose and caribou, which occur in the same region. Infection has not been demonstrated in the small number of specimens of those ungulates examined to date. If, as seems likely, the disease is transmitted chiefly by the respiratory route, the chance of infecting other ungulates is rather slight, since none of them has been observed in close contact with bison. There remains only infection from

contaminated feed, a possibility that is also thought to be small. Moose would be particularly immune to infection in that way because they are predominantly browsers rather than grazers. The danger is greatest for the barren-ground caribou which, like the bison, is a grazing animal. The infection could be acquired on one of its occasional winter invasions of the bison range and then could be spread by direct contact between the highly social members of the caribou herd.

This survey of the importance of tuberculosis does not, in the writer's view, warrant an attempt at the elimination of tuberculosis, which might require virtual elimination of the bison. Elimination is a "shotgun" method, too drastic for the needs of the situation, and particularly objectionable on aesthetic and sentimental grounds. The bison of the park are descendants, at least in part, of the last wild bison, and except for the small Alaskan herd, are the only truly wild bison in existence. To destroy that stock except for the very strongest reasons would be deplorable. Total destruction would also be a costly and very difficult operation and would involve tremendous waste.

Control of tuberculosis may not be required on aesthetic grounds, but it is certainly justified on other grounds. The presence of the disease increases the cost of slaughtering for commercial purposes and results in the waste of a significant amount of meat. Therefore, there is a sound economic reason for instituting control. Tuberculosis also constitutes a threat (a mild one to be sure) to the barren-ground caribou, and that is a valid reason for attempting control in the areas it periodically invades. Fortunately, the areas where commercial exploitation is most feasible are also the areas most frequently visited by the caribou, namely, the Lake Claire meadows and the Salt Plains winter ranges. Control of tuberculosis can be carried out incidentally to any large-scale slaughtering operation as outlined elsewhere in this report. Intensive management practices will be necessary in connection with the program, but they will affect only a small part of the total area of the park, leaving the remainder in its pristine condition for maximum aesthetic enjoyment.

Management for Aesthetic and Historical Reasons

It is quite clear, from the wording of the Order in Council by which Wood Buffalo Park was created, that the chief reason for the establishment of the park was preservation of the bison as a wild species. Wildness is a component of the aesthetic value of the herd. A second reason was to provide for the active enjoyment of the herd by the general public. To date that purpose has not been fulfilled because the park has been difficult of access. However, since World War II there have been tremendous stirrings indicative of a rebirth for the Canadian Northwest. The Mackenzie Highway, the first all-weather road in the Mackenzie District, terminates at Hay River, northwest of the park. A road linking Hay River to Fort Smith is in the planning stage and a link with Fort Vermilion already is under

construction. Those roads will pass through the heart of the northern bison range and will open for the tourist the existing, albeit restricted, network of park roads and trails. The era of participation by the general public in the enjoyment of the wilderness area of the park is now at hand. The aesthetic value of the bison herd, which heretofore has lain dormant, may be expected to reach fruition in the next decade. Bison can be seen behind a fence in a number of easily accessible places in Southern Canada and the United States, and it must be assumed that travellers to Wood Buffalo Park will want to see the species in its natural wild state. Plans for the management of the park as a whole must take this into consideration as a prime objective.

To speak of "managing" aesthetic values is somewhat of a parodox. Aesthetic worth is generally at a maximum when management is at a minimum. With most wild species in National Parks, however, some management must be practised, either to keep the species from disappearing, or, more frequently, to prevent it from over-populating its range. The present situation in Wood Buffalo Park has been shown to involve a herd that is stable or at least changing its numbers so slowly that present census techniques do not measure the changes. It has also been shown that to maintain a steady population both wolves and disease are necessary. Disease may detract slightly from the aesthetic value of the herd, but it appears to be impractical at the present time to control it, except in selected localities. Wolves, in themselves, present an added attraction for many lovers of nature. It is obvious, therefore, that the demands of maximum aesthetic appeal can be met at the present time by a "hands off" policy. This policy should apply to all of the park not specifically set aside for meat production.

A proposal that cuts across several of the prime objectives might also be best considered at this point, since it deals primarily with preservation of the species in the wild state. Bovine tuberculosis is being eliminated from domestic cattle in Canada in a program designed to make the country virtually tuberculosis-free. The question may arise whether the country can be considered tuberculosis-free as long as a wild herd exists as a potential reservoir for reinfection of domestic animals. Agricultural interests may in the future exert pressure to have the situation cleared up. Looking ahead toward that eventuality, it would seem wise to establish a wild herd of tuberculosis-free animals at some suitable place. The country near the source of the Mackenzie River appears suited to bison, and is within the historical range of *Bison bison athabascae*. Besides ensuring the continuation of a wild herd of bison, establishment of a herd in that area should eventually restore the bison to the list of game animals, at least as far as the native hunters are concerned. The suggested area is beyond the range of the barren-ground caribou, which in most other parts of the Mackenzie District is the most important meat animal. As a consequence, there is a perpetual shortage of meat in the area, and even limited supplies of bison would be a welcome addition to the trapper's larder.

Management as a Food Resource

Two types of harvesting may now be considered. First is hunting by holders of general hunting licences, which category does not include all residents of the district, but only those who make their living by hunting and trapping. There are few persons of European extraction among them. The question to be answered is whether they should be allowed to harvest surplus populations of bison outside the park boundaries. The overriding consideration in that case is the presence of diseases communicable to humans. To allow the hunting of animals known to be infected with tuberculosis may seem a dubious practice, especially in the area of the park where the general level of education and sanitation is low and human tuberculosis is a serious public health problem.

Next might be considered the planned management of a part of the herd for maximum meat production. The advantages of such a scheme would be many. Brucellosis and tuberculosis could be virtually eliminated from the managed herds by vaccination of calves and by tuberculin-testing and selective slaughter of reactors. Buffalo meat could be made available throughout the southern Mackenzie District at least. If the meat could be sold at a low enough price, it could be substituted in many cases for caribou meat and thereby reduce the drain on the barren-ground caribou. The offal could be processed as dog feed, thus removing some of the necessity for caribou meat, too much of which is used now for that purpose. Seasonal employment would be provided for some of the local residents. The industry could operate without cost to the taxpayer.

Many of the details of the program would have to be worked out by trial and error; however, enough is known to outline the framework of a feasible scheme.

The obvious first choice of location for the operation was the Lake Claire meadows, with its year-round population of 4,000 to 5,000 bison with the highest reproductive rate of any examined to date. Potentially, most of the bison in that natural unit could be rounded up for testing. Because there appears to be little interchange of animals with other parts of the park, reinfection with tuberculosis could occur only on a small scale, if at all. The chief drawback to the Lake Claire area has been its relative inaccessibility, but this has been overcome by improved winter roads.

A modern abattoir now has been built, and meat is produced under government inspection in order that it may be shipped anywhere in Canada, or exported, depending on available markets. Predators have been controlled in the area as a step in reducing calf losses to the minimum. Some of the aged bison have been eliminated in order to allow their places to be taken by younger more productive animals and thus produce a larger calf crop, but many old animals remain. All animals handled have been tuberculin-tested and reactors slaughtered, and all calves have been vaccinated. By those methods it should be possible to realize an

annual productivity of 20 per cent of the herd strength, or a sustained annual yield of 800 bison per year.

The second choice for that type of management is the Hay Camp area in the Slave River lowlands. One major shortcoming of that area is the fact that the bison that winter there spend the summer in other parts of the park. Thus it would be difficult, if not impossible, to manage them as intensively as the Lake Claire herds. Productivity could be increased by concentrating the slaughter on the old animals, but because only a fraction of the population can be rounded up each year, that would necessarily be a slow process. Similarly, the control of tuberculosis would lag in that area. Almost nothing could be done there to reduce calfhood mortality. The major advantage of the Hay Camp is its accessibility.

From the aerial censuses it was estimated that the bison potentially available for a slaughter at the Hay Camp did not number more than 3,000 before slaughtering operations commenced there in 1952. The herds have been reduced since that date, and it seems unlikely that the sustained yield from the area would rise appreciably above 10 per cent of herd strength, or 200 animals.

A factor that has not been evaluated yet is the effect of a slaughter at Elk Island Park on the markets for the product from Wood Buffalo Park, and vice versa. In the past, the Elk Island slaughter has been biennial and has at times produced as many as 500 carcasses. Because meat of bison appeals mainly to specialized outlets, an additional 800 carcasses from the north might flood the market to the detriment of both operations. In that event, the large kill at Lake Claire could be held biennially when there was no kill at Elk Island, and in alternate years a small kill could be held at Hay Camp with all of the products assigned to satisfy requirements in the Mackenzie District.

Management as a Recreational Resource

The suggestion of sport hunting of bison outside of the park raises two special problems.

The first of these involves tuberculosis. Is it reasonable to expect a sportsman to pay a stiff licence fee to hunt an animal that may be diseased and endanger the hunter's own health? That problem is not insurmountable and could be solved by requiring sportsmen hunting bison to hire a guide instructed in the post-mortem recognition of tubercular lesions. Laymen do much of the routine inspection in meat-packing plants, and there is no reason why they should not function in a similar capacity in the field. In fact, their responsibilities would be less onerous there, because meat would not be an important objective to the sportsman. It would be necessary only to exercise proper caution in preparing the head for a trophy. The sportsmen would be required to employ guides on other grounds as well, so there would be no added cost to them.

The second problem is more subtle. For many years the policy of the Northwest Territories Administration did not permit sport hunting of big game, but reserved this resource for the benefit of the resident hunters and trappers. Those are people with a more or less admixture of Indian and Eskimo blood, plus a few white persons who held trapping rights when the policy was adopted. The result has been that the residents have accepted the idea that big game should be reserved for them, and tend to resent any change.

In spite of this it is apparent that there is a place for trophy hunting in a multiple-use concept of management. Trophy hunters prefer to harvest large bulls, which are practically valueless as meat to the native hunter or to markets. The fact that hunting is engaged in outside the boundaries of the park has ensured that aesthetic values have been maintained. This activity commenced in the autumn of 1959, and there has been an acceptance of it by the local people, who realize that sportsmen bring many values to an area, not the least of which is employment of qualified residents as game guides.

During the first year the number of trophy licences was limited to 30, but this was extended in 1960 to 100. This figure is based on an estimated population of 1,450 bison in the Slave-Little Buffalo lowlands.

Summary of Management Proposals

Canada has an asset of immense aesthetic worth and historical interest in the wild bison of Wood Buffalo Park and the surrounding country. That was recognized in 1893, when legal protection was first provided the bison, and reaffirmed in 1922 with the creation of the park. If the present pace in opening up the North is maintained, the park will be made accessible to the motoring public within the next decade. In a sense, the far-sighted policy instituted so long ago is only now on the verge of being realized, as regards participation by a substantial number of Canadians in the recreational values protected. The first aim of management, therefore, must be to preserve the aesthetic values of the herd. The writer has attempted to show how that can best be accomplished by a "hands off" policy over most of the park area.

In certain areas, notably the Lake Claire meadows and the Hay Camp prairies, conditions are more favourable for intensive management to produce an annual meat crop of considerable monetary value, without materially affecting the aesthetic values to be derived from the remainder of the herd and its occupied range. Testing for tuberculosis and brucellosis, followed by selective slaughters remains a necessary part of the management program. Subsidiary benefits include the provision of seasonal employment for a number of local people, and eventual elimination of tuberculosis and brucellosis from the managed herds. The elimination of disease in those areas will further reduce the already small chance that other

native ungulates might acquire the infection. That is a consideration particularly important with reference to the barren-ground caribou that occasionally invade the bison ranges in considerable numbers.

A second, much smaller harvest taken annually by sportsmen in the Slave-Little Buffalo lowlands outside the park boundaries provides direct income from the sale of licences, and the wages paid to guides.

Finally, the country near the source of the Mackenzie River is suggested as suitable for establishing therein a disease-free herd as additional insurance that the bison may live on as a wild species.

Summary

1. This paper deals with the biology of a herd of hybrid bison (*Bison bison bison* × *B. b. athabascae*), with special reference to the effects of tuberculosis on reproduction, mortality, and management.

2. Physical features and biotic conditions in Wood Buffalo Park are described. The present range is considered adequate. Geological and successional changes will result in loss of range in some areas and gains in others. In the foreseeable future, therefore, the carrying capacity is not likely to change drastically, but population shifts are anticipated.

3. Reproduction was studied in detail. A few yearling males may be capable of productive mating, and a few records of pregnant yearling cows were obtained. About one-third of both sexes matures sexually at two years of age, and the balance at three years or older. The conception rate in a sample of cows of mixed ages was 57 per cent in one herd and 76 per cent in another. No multiple pregnancies were observed in a sample of 481 gravid uteri examined. There was no observed correlation between tuberculosis and lower fertility.

4. Calves constituted 20 to 25 per cent of herd strength immediately after the calving season (early July), but less than 10 per cent by late winter. Yearlings constituted 7 to 9 per cent of the herds segregated, and recruitment into the breeding population is estimated to be between 5 and 8 per cent annually.

5. The incidence and effects of tuberculosis are discussed. About 50 per cent of the old animals in the Hay Camp herd showed visible lesions of tuberculosis on post-mortem examination. The incidence was lower in other herds sampled less extensively. There was no significant difference in the incidence in the two sexes, but generalization was more frequent in females than in males. That may be related to the stress of repeated pregnancies. Mortality from tuberculosis is placed at about 5 per cent per year.

6. Other diseases and parasites found at post-mortem included brucellosis, arthritis, orchitis, metritis, lymphosarcoma, pneumonia, renal calculi, *Damalinia sedecimdecembrii, Setaria labiato-papillosa* and *Dictyocaulus*(?).

7. Wolf predation was found to be most severe on the aged, calves, and handicapped, and is not, therefore, considered a problem. On the contrary, predation appears desirable to help check a too rapid increase in the number of bison.

8. Accidents and catastrophes are considered of negligible importance as mortality factors.

9. A management scheme is outlined, predicated on a multiple-use concept involving aesthetic values, value as food, trophy value, and desirability of protecting other ungulates from tuberculosis.

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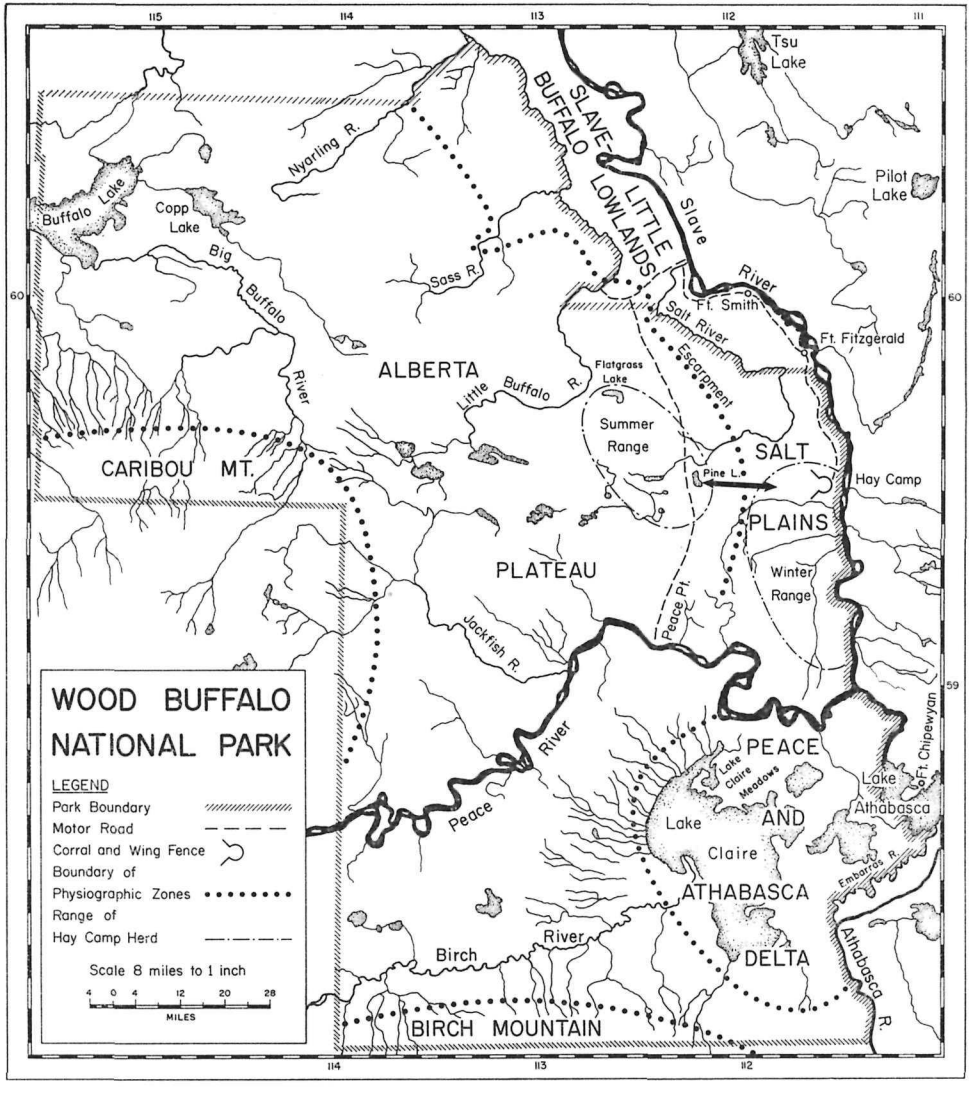
FIGURE 3.

Map of Wood Buffalo Park


115
114
113
112
111
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59
Tsu Lake
Pilot Lake
Nyarling R.
Buffalo Lake
Copp Lake
Big Buffalo River
Sass R.
SLAVE-BUFFALO LITTLE LOWLANDS
Slave River
Ft. Smith
Salt River Escarpment
Ft. Fitzgerald
ALBERTA
Flatgrass Lake
Little Buffalo R.
Summer Range
SALT PLAINS
Pine L.
Hay Camp
CARIBOU MT.
PLATEAU
Winter Range
Peace Pt.
Jackfish R.
Peace River
PEACE AND ATHABASCA DELTA
Lake Claire Meadows
Lake Claire
Lake Athabasca
Ft. Chipewyan
Embarras R.
Athabasca R.
Birch River
BIRCH MOUNTAIN
WOOD BUFFALO NATIONAL PARK
LEGEND
Park Boundary
Motor Road
Corral and Wing Fence
Boundary of Physiographic Zones
Range of Hay Camp Herd
Scale 8 miles to 1 inch
4 0 4 12 20 28
MILES

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