THE ECOLOGY AND MANAGEMENT OF THE AMERICAN BISON

W. A. FULLER
Department of Zoology
University of Alberta
Edmonton, Alberta, Canada.

The American Bison (*Bison bison*) once roamed the continent in millions, but in a few short year of ruthless slaughter this noble creature was brought to the verge of extinction (HORNADAY, 1889). Then, by good fortune, the dedication of several private individuals, and belated action by national and local governments, a tiny remnant of the once great herds was saved in zoos, National Parks, and refuges established especially for their preservation. As an example of the profligate waste of an abundant natural resource, the story of the near extermination of the Bison probably stands unsurpassed in recorded history.

The Bison no longer roams the plains in countless thousands, but its continued existence in federal and state parks, zoos and private herds is assured. There has not been a complete census for several years, but in just the herds under federal control in Canada and the United States there are 20,000 Bison. The herds are widely distributed in the western United States and the prairie provinces of Canada. Beyond the main range of the species there is a small wild herd in Ontario and a somewhat larger one in Alaska.

The populations range in size from small show herds of 8 or 10 to the large wild herd in Wood Buffalo National Park, which is now estimated to contain between 12,000 and 14,000 head (NOVAKOWSKI, 1957). Obviously in a paper of this size I can only deal with a few of the many herds. I have chosen to present in as much detail as possible the results of my own field study of the Bison of Wood Buffalo National Park and the surrounding country. An estimated 2,500 Bison have left the confines of the Park, bringing the total population of the area to

F. Bourlière

F. Bourlière

Rutting time in Bison Range

between 14,000 and 16,500, or about 75 percent of the total North American Bison population. Besides being the most important herd numerically, the northern herd contains the last remnant of the wood Bison (*B. b. athabascae*), which probably represents an intermediate between the wisent (*B. bonasus*) and the plains Bison (*B. b. bison*). For comparison with the northern Bison, as I shall henceforth call the mixture of plains Bison, wood Bison and hybrids in Wood Buffalo National Park, I have chosen three herds of plains Bison, one in Canada and two in the United States. Elk Island National Park, about 20 miles east of Edmonton in central Alberta, contains a herd of between 1,000 and 1,500 Bison. It has an area of about 75 sq. miles (190 Km^2). The next largest herd, of 900 or more Bison, is found in Wichita Mountains Wildlife Refuge, an area of 59,000 acres (26,000 Ha), in southern Oklahoma. The last example that I have chosen is a smaller herd of 325 to 375 on the National Bison Range in northern Montana. The area of that refuge is 18,540 acres (7,500 Ha).

I will first outline what is known of the natality, mortality and population dynamics of the northern Bison, and then attempt some comparisons with the other herds. I will follow the same pattern in discussing management.

Ecology

Wood Buffalo National Park

Natality. — The facts on which this section is based were obtained by examination of carcasses of Bison killed at the annual reduction slaughters for 1952 to 1956 inclusive. During that period 840 mature females were killed and their reproductive tracts were examined. The following information was recorded for each specimen examined : (1) estimated age (see FULLER 1959 for method of age determination) ; (2) presence or absence of milk in mammary gland; (3) presence or absence of a fœtus; (4) crown-rump length of fœtus when present; (5) sex of fœtus; (6) condition of ovaries. From this mass of data, the following conclusions may be drawn.

A single fœtus was invariably found in each of the 481 gravid uteri examined. This confirms and amplifies the conclusions of other American and European workers that twinning is extremely rare in the genus *Bison*.

The primary sex ratio (*in utero*) was found to be 112 males per 100 females or 53 percent males. PALMER (1916) reported a similar primary sex ratio of 54 percent

males (119 males per 100 females) in a sample of 460 Bison. A slight excess of males *in utero* is a common finding among mammals generally.

The age of attaining sexual maturity varies. A few precocious females breed as yearlings at about 15 months of age. Thus, one of 11 yearlings examined was pregnant, and 8 of 177 2-year-olds were lactating, showing that they had conceived as yearlings and produced calves on or about the second anniversary of their own birth. Forty percent of the 2-year-olds examined were pregnant but not lactating showing that they conceived for the first time at an age of about 27 months. Similarly 52 percent of the 3-year-olds were pregnant and not lactating. A few of the latter group may have bred as yearlings and missed as 2-year-olds which would then reduce slightly the proportion of females conceiving for the first time at an age of about 39 months. If the proportion of cows breeding initially at 15 months, 27 months and 39 months is 5 percent, 40 percent and 50 percent respectively, there is a residue of only 5 percent that may breed initially at about 51 months or may be permanently sterile.

Attainment of sexual maturity was studied less extensively in males. A portion of testis and epididymis was preserved from each of 20 young males. Smears were then made and examined for the presence of sperm. The results were as follows : one of six yearlings, three of eight 2-year-olds and all six 3-year-olds, had abundant, apparently normal, sperm in the cauda epididymidis. The situation, therefore, appears to be essentially the same as in females. A small proportion of males attains sexual maturity as yearlings, about one-third as 2-year-olds, and probably all 3-year-olds and older are mature.

The frequency of conception also varies according to the age of the female, as is shown in Fig. 1. The period of greatest reproductive vigour is obviously from three years to the onset of old age (about 15 years ?). During that period of her life each cow would have to conceive, on the average only two years in every three to produce the observed average conception rate of 67 percent. Some measurements of the foetuses carried by lactating cows on the one hand and non-lactating ones on the other hand, shed more light on this question. The data are shown graphically in Fig. 2. The size difference is highly significant for the pooled samples ($P < 0.01$; $t = 5.055$ for 137 degrees of freedom). The simplest explanation for the fact that lactating cows have smaller embryos in midwinter is the suggestion that cows

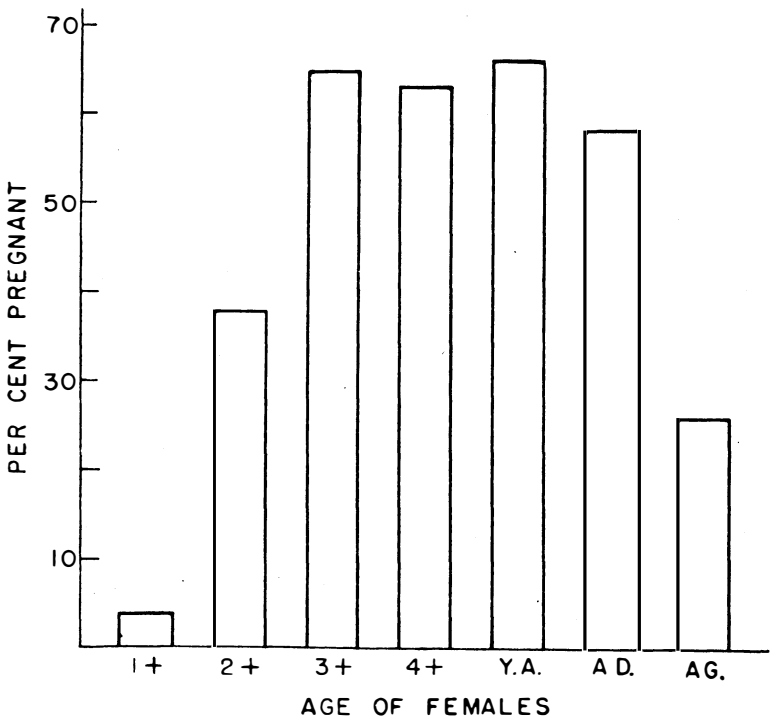

Fig. 1 — Relationship between age and conception rate in 733 bison cows examined at Hay Camp in Wood Buffalo National Park, 1952-56.

accompanied by calves breed later. A virgin cow would probably breed at the peak of the August rut and produce a calf the following May. The presence of the calf seems to reduce the chance that the cow will breed again in August, but there is still a good chance of conception occurring during some later œstrous period. The calf would come toward the end of the calving period, possibly as late as July, which probably precludes August breeding altogether and reduces the chance that the cow will breed during a later œstrous cycle. The following summer, since no calf would be produced, the cow would again be ready to breed in the main August rut. If this interpretation is substantially correct, there is evidence of a fertility regulating mechanism. Survival of a calf apparently reduces the chance that a female will immediately conceive again whereas early loss of the calf probably restores her chances of so doing.

Two diseases, tuberculosis and brucellosis, are present

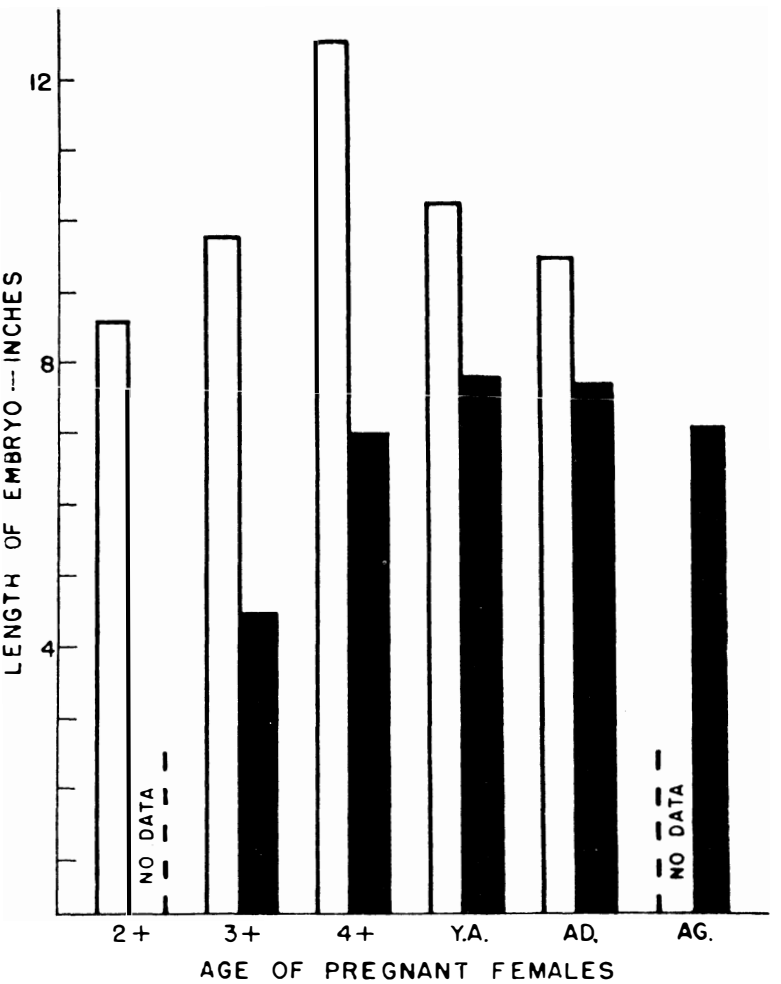

Fig. 2. — Comparison of the length of embryos found in lactating (solid bars) and non-lactating (open bars) bison cows examined during the slaughter of January 1955.

in rather serious proportions in the Bison of Wood Buffalo National Park. Both might be suspected *a priori* of having important depressing effects on fertility. Contrary to expectation, tubercular cows have shown a somewhat higher conception rate than have healthy ones. In one sample 55 percent of 323 tubercular cows and 51 percent of 331 healthy cows were pregnant. This difference is not significant statistically ($P > 0.05$). Probably the shoe is on the other foot—the added physiological stress

may predispose pregnant cows to tuberculosis. Brucellosis was discovered for the first time in 1956, and although nearly 50 per cent of the Bison react to the serum agglutination test, almost nothing is yet known of its effect on fertility.

Mortality. The production of calves has been studied by making counts, either from an aeroplane or from the ground, immediately after the peak of the calving season. Calf production is expressed as a percentage of the total number of animals counted. The maximum proportion observed was 23 percent. This figure is somewhat lower than expected when it is considered that slightly more than half of the cows of all ages were pregnant in mid-winter and that females apparently outnumber males in the herd as a whole. The anticipated calf crop is of the order of 35 or 40 percent of the herd whereas the observed calf crop falls between 20 and 25 percent. The difference may be due to abortion in late pregnancy, that is, after December or early January when the conception rates are obtained, or to *post partum* mortality of calves.

Calf counts made at intervals throughout the year disclosed a gradual attrition. The proportion of calves in the herds declined at the rate of about 2 percent per month. In an average year calves comprised a little less than 20 percent of the herd by September, about 12 percent in December, and 8 percent by late winter. By December calves are becoming difficult to identify in the brief time allowed in an aerial count so the December and late winter figures must be considered conservative. The figures themselves and the sample sizes also varied from year to year, but the general pattern of an initial calf crop exceeding 20 percent of the herd reduced to about 10 percent by the following spring seemed to hold true from 1950 until 1955.

Counts in which yearlings were segregated were even harder to make. In a sample of 1,465 animals compiled by pooling observations for four summers, yearlings comprised an estimated 9 percent. The agreement with late winter calf counts is reasonably good. In the same sample, a class I designated « spike-horns » comprised an estimated 15 percent of the total. The « spike-horn » category consisted mainly of 2 and 3 year olds, so that each contributed 7 or 8 percent. Insofar as these figures have any value they indicate that the mortality rate is much lower among animals over the age of one year. Survival to age one, then, is practically synonymous with recruitment into the breeding population.

Adult mortality is more difficult to measure than calf

mortality, but during the course of my study I was able to identify the important mortality factors. *Post mortem* inspection of the carcasses disclosed a number of diseases and parasites, and field studies elucidated somewhat the role of the wolf (*Canis lupus*) as a predator.

The following diseases and parasites are known to infect Bison in Wood Buffalo National Park :

DISEASES	PARASITES
Tuberculosis	*Damalinia sedecemdecembrii*
Brucellosis	*Setaria labiato-papillosa*
Arthritis	*Echinococcus granulosus*
Arteriosclerosis	? *Dictyocaulus sp.*
Lymphosarcoma	
Pneumonia	
Renal calculi	
Abcesses of undetermined etiology	

Tuberculosis, brucellosis, arthritis and *Setaria* are common, whereas the others are known from only one or a few animals of 1,800 examined. *Setaria,* while of common occurrence, seems to be benign and so will be omitted from subsequent discussion. Arthritis may be a concommittant of either tuberculosis or brucellosis, or it may be a separate disease entity. In either case its chief importance probably lies in predisposing affected animals to wolf predation. The importance of brucellosis is now under study, but no conclusions are presently available. Tuberculosis requires a more detailed discussion.

The incidence of tuberculosis among 1,508 Bison examined at Hay Camp is shown in Table 1. At first sight, the incidence appears to be higher among males than among females. A chi-square test, however, shows that the observed differences are not significant ($P > 0{,}05$). For this reason, the sexes are combined in the third column of the table. The data show that there is at first a tendency for the incidence to increase with age and then a levelling off. The early rise seems to indicate that susceptibility is a function of length of exposure in the young animals. The levelling-off probably has two causes—first, some infected animals will be removed from the sample by death from tuberculosis and second, it seems likely that animals not infected by the time they are 4 years old are genetically more resistant.

Since tuberculosis is a chronic disease, it is difficult to estimate the annual mortality from that cause. I used, as the best available criterion, the proportion of carcasses

TABLE 1

Incidence of Tuberculosis by Age and Sex Among, 1,508 Bison Examined at Hay Camp, 1952-56

Age	MALES		FEMALES		BOTH SEXES	
	Number Examined	% T.B.	Number Examined	% T.B.	Number Examined	% T.B.
Calf	75	23	91	9	166	15
Yearling	138	29	140	37	278	36
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	40	1,508	39

judged totally unfit for human consumption. A carcass is totally condemned when there is evidence of continual haematogenous dissemination of bacilli. At that stage it is generally conceded that the bodily defences of the host are incapable of coping with the disease and the prognosis is negative. The number of total condemnations is shown in Table 2. Some of the variability from year to year may be subjective—different veterinarians differed in the severity with which they judged the carcasses. Partly, too, the age structure of the sample is responsible, because the majority of the condemnations were of animals in the « aged » category. However, the 4-year average of 5.0 percent is the best available estimate of annual mortality from tuberculosis.

TABLE 2

Proportion of Totally Condemned Carcasses in Four Slaughters at the Hay Camp

Years	No. examined	No. condemned	% Condemned
1952	245	9	4
1954	276	9	3
1955	782	54	7
1956	205	3	1
1952-56	1,508	75	5

A second major mortality factor is predation by the timber wolf, *Canis lupus*. Again, information is difficult to accumulate in a large wilderness area. The available evidence on wolf-Bison relationships is summarized below.

During the course of the study, 95 wolves were removed from the Bison range, mostly by poison, and autopsied. Examination of the stomachs showed that 36 were empty except for bait, 39 contained Bison remains, 9 (all from one pack killed on the same bait at the same time) contained moose remains and the rest contained a variety of small mammal remains. Additional evidence came from an analysis of 63 wolf scats found in the summers. (The poisoned wolves were all taken in early winter). Eighty percent of the scats contained Bison hair. Stomach and scat analysis, therefore, combine to indicate that Bison form a staple food for wolves in both summer and winter.

By good fortune I found eleven victims of wolf attacks from which I could learn a good deal. In three cases I interrupted the attack while the victims were still alive. In two other cases the carcasses were still warm when found and in two more, the victims were almost certainly seen alive by other people within 48 hours of their demise. The following information was obtained.

(1) Five of the victims were classed as very old, three were calves and three were in the prime of life.

(2) Two of the three calves bore evidence, in the form of infected cuts, of an earlier wolf attack, showing that even calves do not fall easy prey to wolves.

(3) One very old female also succeeded in beating off one attack before succumbing to a second.

(4) Of the three prime animals, one showed evidence of advanced, generalized tuberculosis, one had a infected bullet wound in the hip, and one had a broken leg. In the latter case, I was unable to determine whether the leg had been broken before or during the wolf attack.

Caution is in order in attempting to generalize from such a small sample. However, 8 of the 11 victims were either calves or very old. Calves are usually produced in excess of requirements for a stable population and the very old animals play a minor role in herd productivity so that predation on these two age classes is least damaging to the general herd welfare. That predation on calves is not excessive is shown by the fact, to be brought out later, that the herd is increasing slowly. Similarly, the presence of a considerable number of very old Bison in the population is evidence that predation on that age class is not

excessive, because excessive predation would remove old animals faster than they could be replaced. Of 3 animals in the prime of life that were killed by wolves, 2 were obviously singled out because they were severely handicapped while the evidence is inconclusive in the case of the third. In summing up it seems reasonable to conclude that the present intensity and age distribution of wolf predation is not detrimental to the population as a whole.

Accidents are probably the only other significant source of natural mortality. So far as is known, these occur chiefly when Bison venture out on thin ice in autumn or on rotten ice in spring. Probably not more than 100 animals or one percent of the herd falls victim to accidents in a year.

In recent years the annual slaughter for management purposes has assumed significant proportions. Before 1950 not more than 50 Bison per year were killed to supply meat to needy Indians or schools and hospitals. Since 1950 kills of 200 to 900 have been made annually. Altogether, just over 3,000 Bison have been removed in the past decade for research and management purposes.

Population Dynamics. If recruitment into the breeding population does not exceed 9 to 10 percent, it is obvious that adult mortality cannot exceed that figure without producing a declining population. This seems an appropriate time, therefore, to look briefly at some population estimates.

Before 1900 the concensus was that no more than 500 *athabascae* were still in existence. Probably as a result of legal protection being extended to them in 1893, their numbers had increased to an estimated 1,500 when Wood Buffalo National Park was established in 1922 (GRAHAM, 1923). From 1925-1928, 6,673 *B. b. Bison* were introduced. SOPER (1941) after an intensive 2 year study, estimated the 1934 population to be 10,000 to 12,000. FULLER (1950), following an aerial count in 1949, estimated a population of 10,000 to 12,500. NOVAKOWSKI (*op. cit*) duplicated the aerial census as nearly as possible and estimated a population of 12,000 to 14,000.

The initial increase from 500 to 1500 in 30 years required a net annual increment of about 7 percent. A continuation of this trend to 1934 with due allowance for the introduced plains animals would have resulted in a figure quite in line with Soper's estimate, but projection to 1949 should have resulted in 25,000 instead of not more than 12,500.

There are two possible explanations for the discre-

pancy. Either my estimate is in error by 100 percent or the rate of growth of the population fell from about 7 percent to nearly zero. Two lines of evidence favour the latter interpretation. The first is Novakowski's independent estimate (*op. cit*) of 12,000 to 14,000, which is still only half of the projected 1957 population on the basis of a 7 percent increment. The difference between my estimate and his is partly brought about by a difference in the treatment of the raw data. A net annual increment of between 3 and 4 percent is required to produce the increase of about 2,000 head estimated by Novakowski, but when only the raw data are considered, the gross increment in 8 years was only 4.2 percent, or roughly one-half of one percent per year. In either case, the increment is considerably less than 7 percent.

The second argument is provided by the statistics of natality and mortality already given. Tuberculosis, reduction slaughters, predation, and accidental death account for nearly all of the estimated recruitment of 8 to 10 per cent.

Summarizing the evidence, it appears that from the 1890's to the early 1930's the northern bison increased at a rate of about 7 per cent per annum, and that from the early 1930's to the present, the herd has increased much more slowly. Since the change came shortly after the introduction of the plains animals, one looks first to that event for a possible cause. The plains animals may have brought with them (1) new genetic material or (2) new sources of mortality. Evidence on the first point is entirely lacking, but it might be suggested in passing that one would expect the result of heterosis to be an increase in fertility rather than a decrease. On the second point there is strong evidence that tuberculosis was introduced with the plains animals and it is probable that brucellosis was as well. The additional mortality produced by the tuberculosis (5 per cent) is almost enough to offset the postulated 7 percent increase. Ordinarily one would expect the population to compensate for the additional mortality, but this response may have been prevented by a concomitant reduction in fertility produced by brucellosis.

While the details may be somewhat obscure, the broad picture appears to be (1) a stable or very slowly increasing population over a period of 25 yars, (2) about half the total mortality caused by tuberculosis, (3) reproduction held in check by brucellosis, (4) predation having a neutral or even beneficial (culling of tubercular animals) effect.

Elk Island National Park.

The second largest herd of bison is at Elk Island National Park, about 20 miles east of Edmonton in central Alberta. That Park is divided into two parts by a major highway. Currently the northern part, about 50 square miles (130 km^2) carries a herd of from 750 to 1,000 bison, while the southern part, about 25 square miles (65 km^2) carries from 300 to 500.

The southern area was established as an isolation area in the late 1940's. It was double fenced and an effort was made to remove all native ungulates prior to the liberation of 65 cows and 10 bulls in 1951. In 8 years the original 75 animals had increased to about 520 and it was necessary to remove 110 to protect the range. This rate of increase—700 percent in 8 years—must be near the maximum potential for the species.

The Elk Island herd is known to be tuberculosis free, but in 1956 brucellosis was detected and the following year a program of calfhood vaccination was adopted. In spite of the presence of that disease 80 to 100 per cent of the cows examined at each slaughter are found to be pregnant.

The only significant source of mortality is the biennial slaughter.

National Bison Range.

The following information was kindly supplied by the Refuge Manager, Mr. C. T. HENRY (in litt.). The population is adjusted to keep it in harmony with the range so that no supplemental winter feeding is required. At the present time it is considered that the range will support between 325 and 375 bison. One hundred and four cows of breeding age produced 100 and 92 calves in 1958 and 1959 respectively. Gross increments in the herd in the last five years have been as follows.

Year	*Herd Size*	*Increment (%)*
1955	310	26
1956	295	27
1957	305	27
1958	317	33
1959	337	26

There is no significant natural mortality.

Wichita Mountains Wildlife Refuge.

This herd originated from 7 bulls and 8 cows donated by the New York Zoological Society in 1907. A brief

history of the herd has been published (HALLORAN, 1957, and HALLORAN and GLASS, 1959). I obtained additional information through the kindness of the Refuge Manager, Mr. Julian A. HOWARD (*in litt.*).

The bison population is held at about 900 which requires an annual disposal of about 250 head. One interesting feature has been the increased fertility in this herd since calfhood vaccination against brucellosis was introduced in 1941. From 1920 to 1940 the calf-cow ratio averaged 34 : 100, whereas from 1941 to 1955 it has averaged 41 : 100.

Again there is no significant amount of natural mortality.

Discussion.

This brief review of the ecology of four major herds of bison discloses both differences and similarities. A basic difference is the location of the herds, stretching from Wichita Mountains in the south (latitude 34° 40') through the National Bison Range and Elk Island National Park in latitudes 47° 20' and 53° 30' respectively, to Wood Buffalo National Park in the north (latitude 58° 10' to 60° 40'). There is a basic similarity, however, in their locations with respect to the great Cordilleran chain of mountains that have an important effect on the climate of North America. All are on or near the eastern slopes, i.e., in the precipitation shadow, and in a region cut off from warm westerly winds blowing in from the Pacific Ocean. Thus, all have a continental type of climate with wide temperature extremes. The extreme highs, surprisingly, do not differ greatly—112° F (44° C) for Wichita Mountains and 103° F (39°C) for Fort Smith at latitude 60° N on the edge of Wood Buffalo Park. There is, however, a rather striking difference in the extreme lows, which are —16°F (—27°C) at Wichita Mountains and —71°F (—57°C) at Fort Smith. The refuges in the United States are hilly with ranges in elevation of 1400 feet (450 m) in Wichita Mountains and near 2000 feet (600 m) in the National Bison range. The Canadian Parks on the other hand are in flat or gently rolling terrain with maximum differences in elevation probably not exceeding 300 feet (100 m).

There are, of course, striking differences in the vegetation. All the refuges under review contain both grasslands and woods, but in Wichita Mountains the woods are of the eastern American type with oaks (*Quercus*

spp.), cedar (*Juniperus*), elm (*Ulmus*), and walnut (*Juglans*), whereas, the National Bison Range and Wood Buffalo Park are dominated by white spruce (*Picea glauca*) and Elk Island Park, in the prairie-forest ecotone contains only scattered spruce in extensive groves of aspen (*Populus tremuloides*). The Wichita Mountains grasslands are a mixture of tall grass prairies and short grass plains, whereas in the other three refuges the grasslands are of the short grass plains type. In Wood Buffalo Park, which has only limited areas of grassland, extensive sedge meadows on recently-formed alluvial lands constitute the most important ranges, particularly in winter.

In spite of these broad differences in climate and vegetation, there seems to be little difference in the ecology of the bison from Wichita Mountains as far north as the plains of central Alberta. The Wood Buffalo Park herd, however, differs strikingly from the rest. In the three southern herds the conception rate approaches 100 per cent and all the cows appear to breed essentially every year. In Wood Buffalo Park the most fertile age-class of cows has only about an 80 per cent conception rate, and over the major reproductive years the cows average only 2 calves in 3 years. Calf production and survival in the southern herds is high resulting in net population gains of 25 to 35 per cent annually, whereas, in the northern herd reproduction is just adequate to offset natural mortality.

Some of the probable causes for the differences are almost self-evident. First, the three southern herds are in fenced refuges with no predators and few, if any, other hazards such as treacherous ice, or extensive bogs. Thus, natural mortality is low. Second, tuberculosis is unknown in the three southern herds, whereas it is a major mortality factor in the northern one. Third, the age structure of the enclosed herds differs from that in the wild herd. The enclosed herds contain proportionately fewer animals in the older age classes, which, in turn, promotes fertility and depresses mortality.

The role of climate and weather factors is more difficult to deal with. Winter cold does not seem to be a problem at Wichita Mountains. On the other hand adequate water was a limiting factor in this region of intermittent streams before the construction of artificial lakes and ponds (see below). Winter conditions are more severe in Montana and Alberta, and probably do not differ very much between the National Bison Range at an elevation of 3,000 to 4,500 feet (900 to 1,450 m) and

Elk Island Park at an elevation of just over 2,000 feet (600 m). The decrease in altitude compensates for the increase in latitude in this case. Winter is a much more severe test, in Wood Buffalo Park than it is at Elk Island, as the following figures from KENDREW and CURRIE (1955) disclose. The daily mean temperatures for December, January and February for Edmonton and Fort Smith, are compared in the accompanying table.

	Edmonton (53°33')		*Fort Smith* (60°00')	
December ...	13°F	—10.5°C	—8°F	—22.2°C
January	6	—14.5	—14	—25.5
February	11	—11.7	—9	—22.8

Weather, *per se,* is probably not an important mortality factor. However, extreme cold undoubtedly imposes a stress by disrupting feeding routines in the face of increased energy requirements, both for maintenance of body temperature and for mobility in the face of drifted snow. This weather-imposed stress probably works in combination with tuberculosis and predators to increase mortality.

The role of brucellosis is even less well understood. In Wichita Moutains there has been increased calf production since the institution of a vaccination program. However, at Elk Island, the conception rate is near 100 percent in spite of a high incidence of that disease. There appear to be some unanswered questions. For example, is the relationship at Wichita Moutains one of cause and effect ? Do the abortions, if any, at Elk Island Park and Wood Buffalo Park, occur in late pregnancy, that is after the reduction slaughters in December and January, the season at which all our data on conception rates have been obtained ?

MANAGEMENT

Wood Buffalo National Park

Management of the northern Bison is a new departure in which the Canadian government is still just feeling its way. There seem to be several important considerations, but all can be combined in a multiple use concept. The presence of tuberculosis and brucellosis is a complicating factor that must be kept in mind throughout the discussion.

If the area of occupied ranges beyond the Park boundaries is added to the area of the park, the total area of the northern Bison ranges approaches 20,000 sq.

mi. (51,800 km^2). In an area of that size with a diversity of habitats and much variation in the density of the Bison population, there is obviously room for more than one form of management. Most important in my view, is the continued preservation of the Bison for aesthetic and historical reasons. It was for those reasons that legal protection was given to the surviving wood Bison in 1893. In 1922, the same reasons influenced the government of the day to set aside Wood Buffalo National Park as an additional safeguard. In all those years only a small fraction of one percent of Canadians have ever visited the park and seen the Bison. But now, with the construction of roads into the north, Wood Buffalo National Park is at last becoming acessible to anyone with an automobile.

It must be assumed that anyone who travels to Wood Buffalo National Park wishes to see the Bison in their natural state, since captive herds are to be seen in many more southern locations. It is seldom possible to allow ungulate populations to develop in parks without artificial population controls. All the evidence so far obtained in Wood Buffalo National Park, however, points toward a nearly stable population, probably as a result of the interplay of tuberculosis, brucellosis and predation. Over most of the range, the population seems to be well within the carrying capacity of the habitat. Over most of the range, too, the animals are rather thinly distributed, so that any form of management, besides being unnecessary, would be difficult and costly.

In a few places, however, the population in concentrated in especially favourable habitats such as the extensive sedge meadows on the flood plains of the major rivers, and a few grassy prairies. Concentration of the population poses a threat to the range and also means that intensive management can be carried on more easily and at lower cost. On the sedge meadows of the older parts of the delta of the Peace River there is a year-round population of 4,000 to 5,000 Bison. Here, a modern abattoir, corrals, and holding pens have been constructed. With the facilities available at this location hundreds of Bison can be captured, tested for tuberculosis, inoculated against brucellosis, permanently marked and then released or slaughtered. There are sound reasons for hoping that selective slaughter of reactors to the tuberculin test over a period of years will result in near elimination of that disease in the managed portion of the herd. Similarly, calfhood inoculation against brucellosis should reduce the incidence of that disease. The combined result should be

increased productivity, leading to greater meat production with less diseased meat to lower the profits, and eventual operation of the management program on a financially sound basis. This means that the management program should cease to be a burden on the tax payer.

Another valid management objective is to return the Bison to the list of game animals in Canada. There are an estimated 2,500 Bison outside the Park boundaries that could form the basis for a considerable trophy hunting industry. In order to ensure a continuing supply of trophy heads the quotas will need to be carefully controlled. The initial hunt, the first in Canada since 1893, took place in September and October of 1959. Only 30 licences were issued and 30 trophies were secured.

Finally, recent investigations (Banfied and Novakowski, *op. cit.*) have shown that a small population of pure wood Bison still survives in the northwest corner of the Park. Presumably, those animals have had little or no contact with the introduced plains Bison and so may also be free of tuberculosis and brucellosis. The Canadian government is now considering establishing a herd of disease-free wood Bison on a suitable range removed from all possible contamination by the plains Bison and their diseases.

Elk Island Park

The chief management procedure is a bienial slaughter at which the population is reduced below 1,000 animals. For many years supplemental winter feeding has been carried out because the combined population of Bison, moose (*Alces americana*) ,wapiti (*Cervus canadensis*), and deer (*Odocoileus virginianus* and *O. hemionus*) exceeds the carrying capacity of the range. Consideration is now being given to reducing the animal populations to the point where supplemental feeding will no longer be necessary. Periodically the entire herd has been tested for tuberculosis and found to be free of that disease. Since the discovery of brucellosis, a program of calfhood vaccination has been instituted.

United States Herds

The policy in all the U. S. refuges is to carry only as many animals as the range will support. In order to implement that policy, disposal programs are carried out annually. Long yearlings (about 18 months old) are sold alive to private individuals for propagation or

donation to parks and zoos. The demand for live animals is insufficient to accomplish the desired reduction so that additional animals must be slaughtered. The meat is sold to individuals or groups. Hides and heads either accompany the carcass or are disposed of separately.

Another universal practice is vaccination against brucellosis. Vaccination will be required as long as brucellosis is present in domestic stock because of the ever-present danger that one of the hundreds of thousands of visitors might contaminate the range with material carried on vehicles, clothing or shoes.

The most varied management program has been practiced at Wichita Mountains. The carrying capacity of the range for Bison has been raised by the artificial creation of lakes and ponds with a surface area of over 600 acres (255 Ha), and the control of pest plants. All calves are branded with the last number of the calendar year of their birth. A running total of all sex and age groups and all additions or removals is calculated monthly. An effort is made to keep representatives of all age groups on the range, and the sex ratio is maintained at 2 males for each 3 females. A greater proportion of females would undoubtedly lead to more rapid increase, but that would be more of a detriment than an advantage. Finally, an attempt is being made to increase the size of the individual animals by selectively culling the smaller ones for disposal and saving the largest for breeding.

Summary

This paper outlines in some detail the population dynamics of a large, free-ranging herd of Bison in Wood Buffalo National Park in northern Canada. That herd increased from a remnant of about 500 in the 1890's to an estimated 1,500 in 1922. In the late 1920's 6,600 plains Bison were added to the original population of wood Bison. Since 1930 the increase has been much slower, probably because of increased mortality caused by tuberculosis and reduced fertility caused by brucellosis. Both diseases were probably introduced with the plains Bison. In contrast, the rate of increase of three small, fenced herds of plains Bison is about 25 percent per year.

Management of the fenced herds consists mainly of periodic reduction in numbers to keep the population within the carrying capacity of the range.

Management of the wild, northern Bison entails

mainly an attempt to reduce the incidence of tuberculosis in certain selected portions of the herd. A minor, but still significant management goal is to restore the Bison to the list of game animals by permitting the hunting of trophy bulls in areas outside the Park boundary. The bulk of the herd is being left in as nearly a natural state as possible in order to reap the maximum aesthetic benefits.

At present there are about 20,000 Bison under federal government protection in the United States and Canada plus others under State, Provincial or private control. The herds are widely distributed in the western part of the continent and the future of the species seems assured.

REFERENCES CITED

BANFIELD, A.W.F. and NOWAKOWSKI, N.S. 1960. The survival of the wood bison (*Bison bison athabascae Rhoads*) in the Northwest territories. *Nat. Mus. Canada, Nat. Hist. Papers,* n° 8 : 1-6.

FULLER, W.A. 1950. Aerial census of northern bison in Wood Buffalo Park and vicinity. *Jour. Wildlife Manag.,* 14 : 445-51.

FULLER, W.A. 1959. The horns and teeth as indicators of age in bison. *Jour. Wildlife Manag.,* 23 : 342-44.

GRAHAM, M. 1923. *Canada's Wild Buffalo.* Canada, Dept. of Interior, Ottawa. 12 pp.

HALLORAN, A.F., 1957. The bison returned to the plains. *Animal Kingdom* (Bull. N.Y. Zool. Soc.), 60 : 130-34.

HALLORAN, A.F. & BRYAN P. GLASS. 1959. The carnivores and ungulates of the Wichita Mountains Wildlife Refuge. Oklahoma. *Jour. Mammal.,* 40 : 360-370.

HORNADAY, W.H. 1889. The extermination of the American Bison with a sketch of its discovery and life history. *Smithsonian Rept. for 1887,* pt. 2 : 367-548.

KENDREW, *W.G.* and CURRIE, B.W. 1955. *The climate of central Canada.* Queen's Printer, Ottawa. 194 pp.

NOVAKOWSKI, N.S. 1957. Aerial survey of bison in Wood Buffalo National Park and surrounding areas. Unpubl. Rept. in files of Canadian Wildl. Serv. 12 pp. typescript.

PALMER, T.S. 1916. Our National Herds of Buffalo. *Ann. Rept. Am. Bison Soc.,* 10 : 40-62.

SOPER, J., DEWEY. 1941. History, range and home life of the northern bison. *Ecol. Monog.,* 11 : 347-412.