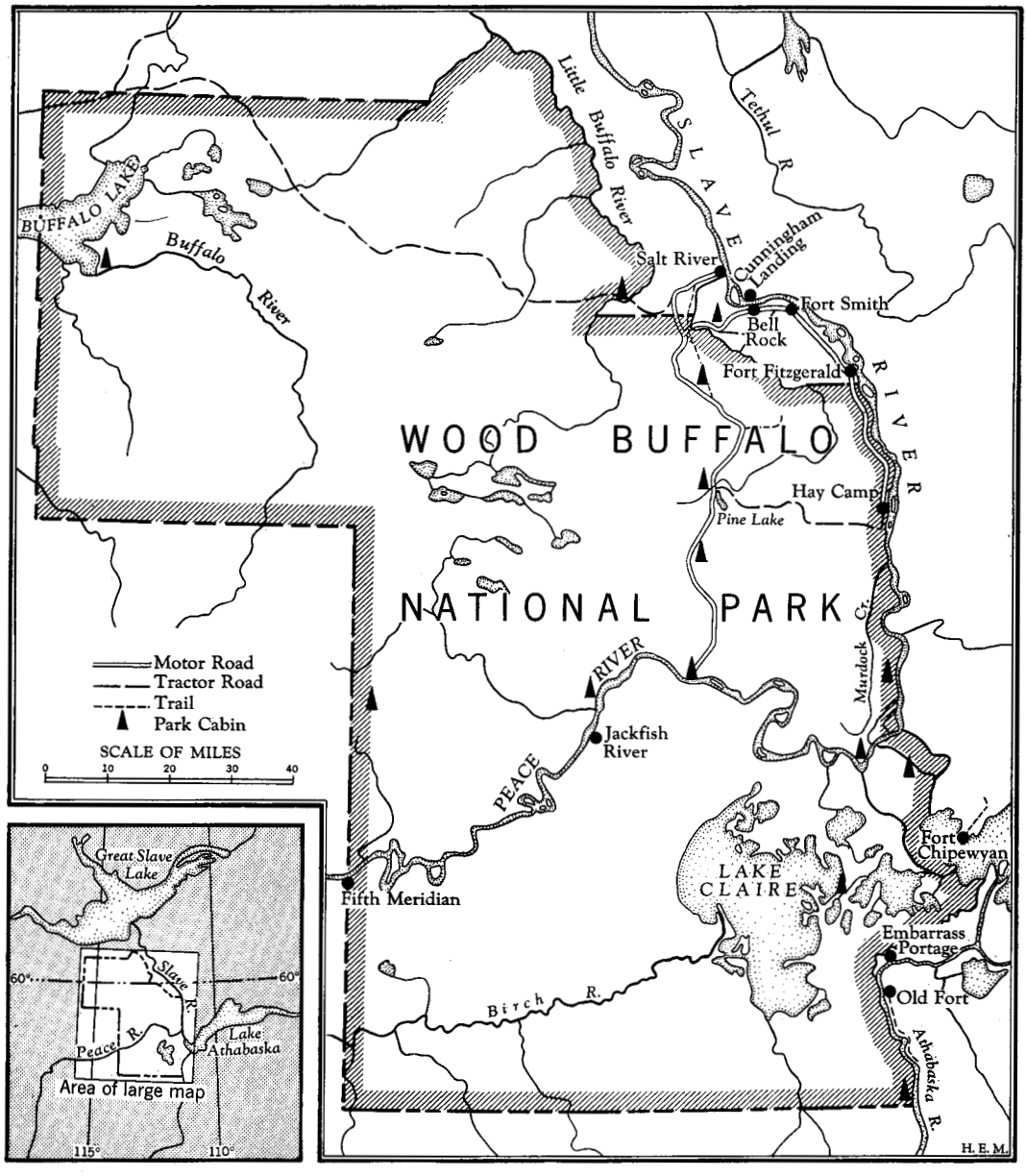

Fig. 1. Map of Wood Buffalo National Park.

BEHAVIOUR AND SOCIAL ORGANIZATION OF THE WILD BISON OF WOOD BUFFALO NATIONAL PARK, CANADA

W. A. Fuller*

FROM 1950 to 1956 I was engaged in a study of the biology of the bison in Wood Buffalo National Park with particular reference to the effects of tuberculosis. During this time I had many opportunities to observe their behaviour. The purpose of this report is to record my observations.

Wood Buffalo National Park (Fig. 1) was originally set aside in 1922 for the protection of the last remnant of the wood bison *(Bison bison athabascae)*. However, in the years 1925 to 1928 inclusive, more than 6,000 plains bison *(B. b. bison)* were introduced into the park where they interbred with the estimated 1,500 remaining wood bison. The population now in the park is considered to consist almost entirely of a mixture of the two races. Animals closer to the plains type predominate. The animals are completely in the wild state. A few hundred are rounded up annually and held in corrals for a few weeks before slaughter. There are no other fences, and supplementary feeding is neither required nor practised. All observations refer to free-ranging bison unless the corrals are specifically mentioned.

I. Behaviour

Roe (1951) states that much of the evidence concerning the habits of the bison is contradictory. He documents this by extensive quotations from earlier literature in his chapters five, six and seven. The contradictions are readily understood if one remembers that the plainsmen of the nineteenth century were not, for the most part, trained and critical observers. Even Hornaday (1889), one of the few trained zoologists to study the bison during this period, was guilty of accepting dubious evidence at its face value and thus helping to perpetuate a number of fallacious beliefs. In a later book (1922), he showed himself to be a close observer of certain aspects of the behaviour of captive bison. Similarly, Garretson (1938), whose book is weak in many respects, was surprisingly accurate in his brief descriptions of behaviour. Seton (1929), although generally accurate, has uncritically quoted some doubtful statements of earlier writers, thereby implying his acceptance of their beliefs.

* Formerly Can. Wildl. Service, Whitehorse, Y.T.; present address: Dept. of Zoology, University of Alberta, Edmonton, Alta.

Two investigators of the northern bison have published reports that dealt in part with behaviour and social organization. Goodwin (1935, 1939) wrote semi-popular accounts of the Snyder expedition, whose chief purpose was to secure museum specimens. Soper (1941) published a detailed account of his two-year study of the bison including many references to behaviour. The most complete description of bison behaviour is the recent work of McHugh (1958).

Characteristics of bison that influence behaviour

Senses. The capacity of an animal to adjust to its environment, either physical, biological, or social, depends in large measure upon the possession and relative development of sense organs. Those forms with well developed senses are better equipped to detect changes in the environment (stimuli) and make satisfactory adjustments (behaviour). In general, the senses of the bison are well-developed. McHugh (1958) found that bison detected a moving jeep at distances of more than a mile and a horse and rider at 0.8 mile. I have had similar experiences on foot and with motor vehicles of various types. I have noticed that the flight distance is usually greater from a man on foot than from a motor vehicle. It is apparent, therefore, that bison can see, and distinguish between, objects at considerable distances.

As might be expected from the prominent external ear the sense of hearing is also acute in bison. They react to small noises such as the accidental cracking of a branch underfoot at distances of 100 to 200 yards. On cold winter days the noise of frozen branches brushing against heavy clothing can also be detected by the animals for some distance and this will often spoil a stalk. On one occasion I was watching a herd of bison and noticed that they began to focus their attention in my direction, but were looking beyond my hiding place. After some time I heard bison vocalizing and later a second herd appeared from the surrounding woods. Since there was a cross wind it is evident that the first herd initially detected the presence of the second by auditory stimuli. It is equally apparent that the bison reacted to the sounds of the second herd long before those sounds were audible to me.

The sense of smell is highly developed and appears to be of prime importance in detecting danger. Bison will frequently permit a guarded approach by a person that they have detected either by sight or hearing, but I cannot recall an instance of hesitation once they had caught my scent. On this point McHugh (1958) stated "Whenever scenting humans the Hayden Herd stampeded without hesitation even though the source of scent was not visible". I have seen many striking examples of this. On one occasion, after watching a herd from a place of concealment for nearly an hour, a sudden shift in the wind, which carried my scent to the bison, precipitated an immediate stampede. I have no quantitative data on the maximum distance at which bison can detect human scent, but it is at least several hundred yards.

The chemical senses are also used by males to detect a female in heat. They may also be important in individual recognition, for example the identification of a calf by a cow following temporary separation. I have even seen two adult males approach and smell each other in a manner reminiscent of dogs.

The sense of touch seems to be of minor importance in bison behaviour.

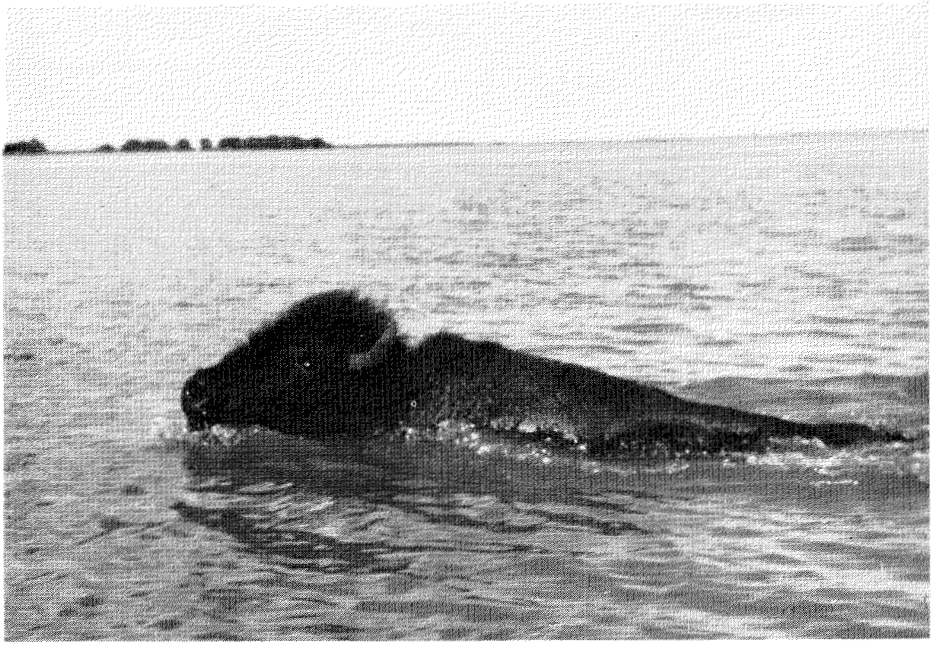

Fig. 2. Bison cow swimming in Lake Claire.

Locomotion. Bison, in spite of their ungainly appearance, are swift runners. When "pushed" from behind by a truck with a horn blaring and people shouting they are capable of a top speed of between 30 and 35 miles per hour and they can maintain such an all-out effort for up to half a mile. There seems to be no significant difference between the top speed of males, females, and calves only a few weeks old. Even calves so young that a few inches of the umbilical cord are still visible, can keep up with the herd for short distances.

Bison are also powerful swimmers. When swimming the hind quarters are low in the water and only the head and top of the hump show. I observed a lone cow swimming strongly from the mainland to an island in Lake Claire, a distance of about a mile and a half (Fig. 2). I followed her in a canoe and noted that she showed no undue signs of fatigue on landing. Bison also regularly swim the Peace and Slave rivers, which are approximately half a mile across and have currents running from 2 to 4 miles per hour.

Vocalization. Bison are capable of producing a number of sounds. The "bellow" is the one best known. It is heard most frequently as the rutting season approaches and seems to be a manifestation of the increasing restlessness of the males. Two other sounds are made frequently by males and less frequently by females. The "snort" can be imitated by forced inhalation with fluttering of the soft palate and the "cough" by forced exhalation past a glottal stoppage. "Snorts" and "coughs" are associated with agonistic (fighting) behaviour. I have rarely heard any of the grunting sounds described by McHugh (1958) except from animals being herded around in the corral.

Cows searching for lost calves have been heard to utter a series of snorts. Calves have not been heard to respond in the wild, but in the corral they do a good deal of bawling.

Anatomical peculiarities. Two structures possessed by bison play a prominent part in certain types of behaviour. The horns, efficient weapons for fighting, are prominent in agonistic behaviour. They are also used to dig or at least scratch the surface of wallows (grooming behaviour) and in horning trees (possibly a type of "displacement activity").

In this region, with its hordes of biting insects, the importance of the tail as a fly switch is obvious. The tail also functions less obviously as an indicator of the emotional state of the animal. In any situation involving the attack-escape drive the tail is held erect. Males showing investigative sexual behaviour also usually carry the tail erect or partly erect.

Social behaviour

Scott (1958) classifies all behaviour under nine headings. I have data that have a bearing on social behaviour under five of these headings.

Epimeletic (care-giving) behaviour. Adult males indulge in a considerable amount of grooming particularly in the summer months. Ordinary grooming consists of rubbing against stumps, trees, or rocks, and wallowing. These mannerisms are well known and have been described by Soper (1941) and McHugh (1958). I observed one instance of what I interpreted as mutual grooming of two adult males. These two exchanged gentle horn digs in the thorax and abdomen. This exchange was not accompanied by any aggressive actions. The result appeared to be mutually pleasurable and may have been similar to the sensation achieved by rubbing against trees or rocks.

Females do much less wallowing and rubbing than males. Their chief expression of care-giving behaviour is through nursing the young. Although I found solid food in the stomachs of calves shot in July for disease studies, weaning seems to be a protracted affair. The udders of cows shot in January contained copious amounts of milk and milk could be expressed from the nipples by hand.

Females are also concerned with the defence of the calves, both from natural predators — wolves — and from humans. I recorded one instance

of a cow remaining with a calf crippled by wolves. My fortuitous appearance frightened away the wolves (of which I glimpsed two) and started a stampede among the bison. One cow remained behind, and when I sought a reason for her refusal to leave, I found the nearly dead calf lying behind a fallen tree. On one occasion I was threatened and driven off by a cow when I attempted to photograph and capture a young calf that had become exhausted during a chase by motor vehicle. Another time, after I had shot a calf for a *post mortem* examination a cow would not let me approach the carcass. After several attempts to do so had failed the cow finally had to be shot.

Seton (1929), Garretson (1938) and Soper (1941) have all pictured the bulls as defenders of the young. I have seen no indication of this in Wood Buffalo Park, nor did McHugh (1958) in the herds he studied.

Allelomimetic (contagious) behaviour. Allelomimetic behaviour occurs in two important situations — in the disorderly type of escape known as a "stampede", and in winter when a herd must travel through snow. The question of leadership is closely related to this form of behaviour. Soper (1941) and Seibert (1925) attributed the position of herd leader to a "majestic bull" whereas McHugh (1958) thought that "cow groups" were most frequently led by older cows. My observations suggest that in mixed groups the situation determines the leader in no small degree.

When breaking trail through new snow a bull (or bulls if more than one is present) is usually in the van and the weaker animals string out behind. If the group is small the animals proceed in single file whereas larger groups may proceed two or more abreast. The adaptive value of this arrangement is obvious.

Two patterns of flight behaviour have also been noted. Usually when the herd is approached in the open I agree with McHugh that the older cows are the most alert members of the group and are likely to take the lead in the ensuing "stampede". I noted a different reaction, however, when groups were surprised on the twisting fire trails through the park. Frequently the herd retreated down the road and disappeared from view around a bend or over a slight rise. Once out of sight of the source of danger the herd paused. If the observer followed along the road, he would see first a mature bull facing in his direction. Fifty to one hundred yards down the trail the rest of the herd would be closely bunched, usually facing away from the observer, but looking back over their shoulders. At the first appearance of the observer, the "rear-guard" bull would wheel and run in the direction of the herd. The wheeling of the bull appeared to be the signal for the herd to retire. A herd disturbed a second time in this manner rarely paused again until it had travelled some distance into the shelter of the forest. The pause after the first short flight seemed to serve the purpose of confirming that a real source of danger existed. The bull assumes the function of a leader in this case even though he is bringing up the rear.

On this point Soper (1941) says "he [the bull] is more often the one to leave last as the animals take fright and dash away together into the woods". The only other mention of a similar behaviour that I have seen is by Grinnell (1904) who thought that the bulls brought up the rear simply because they were slower, and not from any "desire" to protect the herd.

Allelomimetic behaviour is prominent in the play activities of calves. Games of "follow the leader" and sudden sprints and chases are common forms of play.

Agonistic behaviour. An aggressive attitude is displayed chiefly by posture. Vocalization ("coughs" and "snorts") accompanies the threat posture in a minority of cases. A mild threat is conveyed by the rigidly erect tail. With increasing stimulation of the attack-escape drive the head is lowered and, usually, swung slowly from side to side. Finally, the threatening bull, with tail up and head down, paws the ground with a fore foot.

There is lack of unanimity among observers as to whether or not fighting bulls charge one another. Goodwin (1935), Cahalane (1947), and McHugh (1958) all mention charges. My observations, however, agree with Garretson (1938) and Hornaday (1922) who state that the animals advance slowly. In fact, the actual encounters that I saw had a stylized appearance. Heads were lowered and carried slightly to one side; the animals advanced and locked one horn; there was some minor shifting as though to find a comfortable position for the locked horns, and the battle commenced. There resulted a shoving match, with the object apparently of turning the opponent broadside in order to deliver a telling blow. Should the contact of the horns be broken, it was carefully rejoined by the method described. The longest battle I witnessed lasted approximately 5 minutes during which time the larger of the two combatants pushed the smaller across a road, down through a 4-foot ditch and about 30 yards across a prairie. The smaller animal was holding its own on level ground when the encounter came to a sudden and (to me) unexpected end.

Aggressions among males, are not restricted to the breeding season, but seem to increase in frequency at this time. Soper (1941) stated that there were "many battles" during the rut, but my observations fail to substantiate this. Much depends on the interpretation of the word "many". In my experience most encounters between bulls are decided by threats (McHugh's "passive dominance") and never reach the fighting stage. This implies that dominance relations are well defined. Wardens and other casual observers frequently described to me vicious battles they had seen. It is only natural that they should be impressed by the occasional fight, but not by the more frequent encounters wherein no fight ensued. Soper depended on the testimony of wardens to support many of his observations, and this may have led him to overemphasize the occurrence of battles during the rut.

One other situation seemed to stimulate attack and escape drives simultaneously — the sudden intrusion of a loud noise. Nearly always

when "buzzed" by a low-flying plane any bulls that happened to be close to each other engaged in battles, lasting only a few seconds, before turning and fleeing. The same behaviour was frequently observed in groups of bison standing on the road when I came suddenly on them in a noisy truck (a Power Wagon). I observed it once in a group standing near the bank of a narrow river when I rounded a bend in a canoe propelled by an outboard motor.

Aggressions between females were not infrequent but they occurred so unexpectedly (i.e. without preliminaries) and were so quick and brief that I was unable to note details.

Sexual behaviour. The earliest indication of the onset of the rut is an increased restlessness in the bulls; this is shown in two ways — first by uprooting small trees, generally spruce seedlings 3 to 5 feet high, and second by increased vocalization. Both these activities take place mainly at night. By day there is little or no change in the tenor of the herds likely to be noticed by the casual observer. The preliminaries to mating are only seen if one watches an undisturbed group for some time.

The sexual actions of the males later in the rut are quite characteristic. A male approaches a female with his neck lowered, head extended, lip upcurled, tail partly or fully erect, and smells her external genitalia or freshly voided urine. A bull may investigate several females in this manner in a short space of time or he may stay close to one cow. McHugh (1958) called this latter type of association a "tending bond". He found, as I did, that most tending pairs took up a position near the periphery of the group. In this study, and in McHugh's, only fully mature bulls were observed to tend a cow. McHugh also recorded several examples of atypical tending bonds. While I did not observe anything of this nature, I do not consider my observations to be extensive enough to rule out the possibility of atypical tending bonds occurring in the northern bison.

I have seen a tending bull direct a cow by placing his extended chin against her head and gently forcing her to turn through 90 degrees. He then resumed his place at her side and began licking her flank. On another occasion, a bull "nuzzled" a cow in the neck, forcing her to turn her head, whereupon he began to lick her cheeks and chin. These actions could be described as "amatory" behaviour.

I observed many attempted mountings but did not see any complete copulations.

Seton (1929) has labelled the type of mating of the bison polygamous (more precisely, polygynous), and with this most modern writers have agreed. The herds, at the time of the rut, contain many more mature females than males, an observation that seems to support this thesis. However, I have shown (Fuller 1957) that by no means all cows conceive each year — only a little more than half the cows in the Hay Camp herds, which have been studied most intensively. The ratio of males to receptive cows, therefore, is much closer to equality, so that the sex ratio of a herd, in itself, proves nothing. Pre-copulatory behaviour is also inconclusive, since

bulls have been observed to tend several cows in rapid succession. The question can only be definitely decided by observing how many cows are served by one bull. I have had no opportunity to make these observations, perhaps because, as suggested by several writers (e.g., Cahalane, 1944), mounting occurs most frequently at night. McHugh (1958) classed the type of mating in a confined herd as temporary monogamous. He thinks the bulls are promiscuous, but that a given cow is served by only one bull.

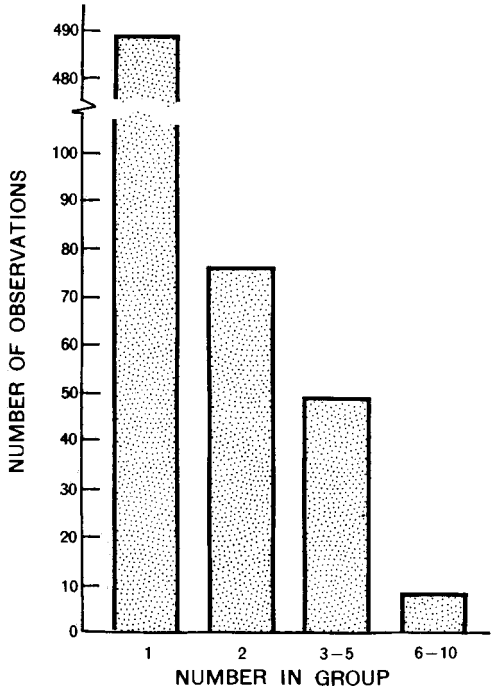

Fig. 3. Frequency of occurrence of groups of male bison in forested habitats.

II. Social organization

Herd composition

McHugh (1958) classified buffalo into bull groups and cow groups according to composition. I prefer the term "mixed group" to "cow group" for the northern bison because these herds nearly always contain some mature males as well as mature females and young of both sexes.

My observations on groupings were made mainly in the summer season from June to September because it was only at that season that the animals could be conveniently studied on the ground. Observations made from planes at other seasons of the year, however, indicated that the bull groups and mixed groups remained apart throughout the year.

Bull groups. In forested habitats the bull groups I observed never contained more than ten individuals. Road counts in the forested habitats from 1950 to 1953 inclusive yielded 488 lone bulls, 88 groups of two, 49 groups of three to five, and only 9 groups of six to ten (Fig. 3). Bull groups tended to be larger on the meadows bordering Lake Claire. The largest bull group I observed was seen there from a plane and contained 30 members. Groups of 15 to 20 are relatively common. McHugh (1958) found the bull groups in Yellowstone Park to be composed of one to twelve members.

The totals presented are biased by an unknown amount of duplication. The sandy roads seemed to attract the bulls, probably because of the ease with which dust wallows could be made in them. The ditches and spoil-banks were also much used by the bulls for resting areas. Thus the bull groups tended to stay on or near the roads and the same groups were probably tallied several times. For example, a lone bob-tailed male, probably the same individual in each case, was observed at approximately the same place six times in the month of August, 1954.

Old age was not the rule among the lone bulls. Approximate ages, based on horn wear, (Fuller 1959), were assigned to 370 of the 488 observed. Of these, 34 per cent were 7 years or older, 65 per cent were 4 to 6 years old (i.e. just reaching full maturity) and the remaining 1 per cent were 2 and 3 year-old spike-horns. These figures contradict the thesis put forward by many writers, including Goodwin (1939) and Soper (1941) for the northern bison that the lone bulls are old animals driven from the herd by younger mature bulls.

Spike-horn males (2 and 3 year-olds) either remained in the mixed herds or were associated with the larger bull groups. They were seldom found alone (see above) or as members of a pair. These observations agree with McHugh's (1958) for Yellowstone Park buffalo.

Mixed groups. Age and sex counts were made for the most part along the narrow roads in forested terrain. Some members of a herd frequently remained among the trees where they could not be identified as to age and sex, and therefore the counts were seldom complete. The most nearly complete segregated counts obtained during the summers of 1950 and 1953 are shown in Table 1. No winter counts were made.

Slightly over 86 per cent of the animals in these counts were classified as to age and sex. To disregard the remaining 13.6 per cent would introduce a bias because it is known that they were mostly mature females and immatures of both sexes — the groups most difficult to separate. Therefore, an attempt has been made to distribute these animals among the other classes (Table 1, column 3). These adjusted totals are open to some objections, but they are in my opinion more meaningful than the unadjusted ones.

A primary sex ratio of 112 males to 100 females was determined from a total of 472 foetuses examined during the annual slaughters. The secondary sex ratio was not determined because the nervousness of herds

Table 1. Sex and age counts of bison recorded during the summer months, 1950 to 1953, inclusive.

Age	*Observed total*		*Adjusted total*	
	number	*per cent*	*number*	*per cent*
Calf	223	15.2	240	16
Yearling	112	7.6	135	9
Spike-horn	165	11.3	220	15
Adult and aged male	292	19.9	310	21
Adult and aged female	473	32.3	560	39
Unclassified	200	13.6	—	—
Totals:	1,465	99.9	1,465	100

with new calves precluded the prolonged study necessary to differentiate the sex of the calves. Eighty-seven spike-horns were sexed giving a ratio of 55 males to 32 females. This ratio is undoubtedly biased by the greater ease of identifying the males with their slightly larger body size and more conspicuous horns. There is no apparent reason why this ratio should depart significantly from equality. The sex ratio among adults in mixed herds (Table 1) is about five to three in favour of the females (60 males to 100 females). What part of this inequality is made up by the bull groups is difficult to state because of the tendency of the bulls to congregate along the roads and thus be counted repeatedly. It is my impression that there are too few bachelor bulls to make up entirely the deficit of bulls in the mixed herds.

Figs. 4 and 5 show in graphic form the information on herd size. Fig. 4 refers to the forested areas where the data were gathered by means of road counts in the summers only. In this habitat the herds tended to be small in size. More than one-half of the herds observed contained between six and twenty individuals and less than one-third contained more than twenty. Fig. 5 shows the frequency distribution of herds of various sizes on the open sedge meadows north of Lake Claire as counted from a plane. In this habitat the herds tended to be larger in size — nearly two-thirds of the herds contained more than twenty individuals. It will be recalled that the same tendency was noted in bull groups. Fig. 5 also shows that there is much variation in the size of the herds on the meadows from time to time, indicating that joining and splitting of herds is common. I believe that joining and splitting also occur frequently in the forests but my data are inadequate to demonstrate it there.

In both Fig. 4 and Fig. 5 the 11-20 class appears to constitute a well-marked "mode". However, since the class intervals are not all the same, a strict definition of the term "mode" does not apply. If a 1-10 class had been used it would contain the greatest frequency of observations in Fig. 4,

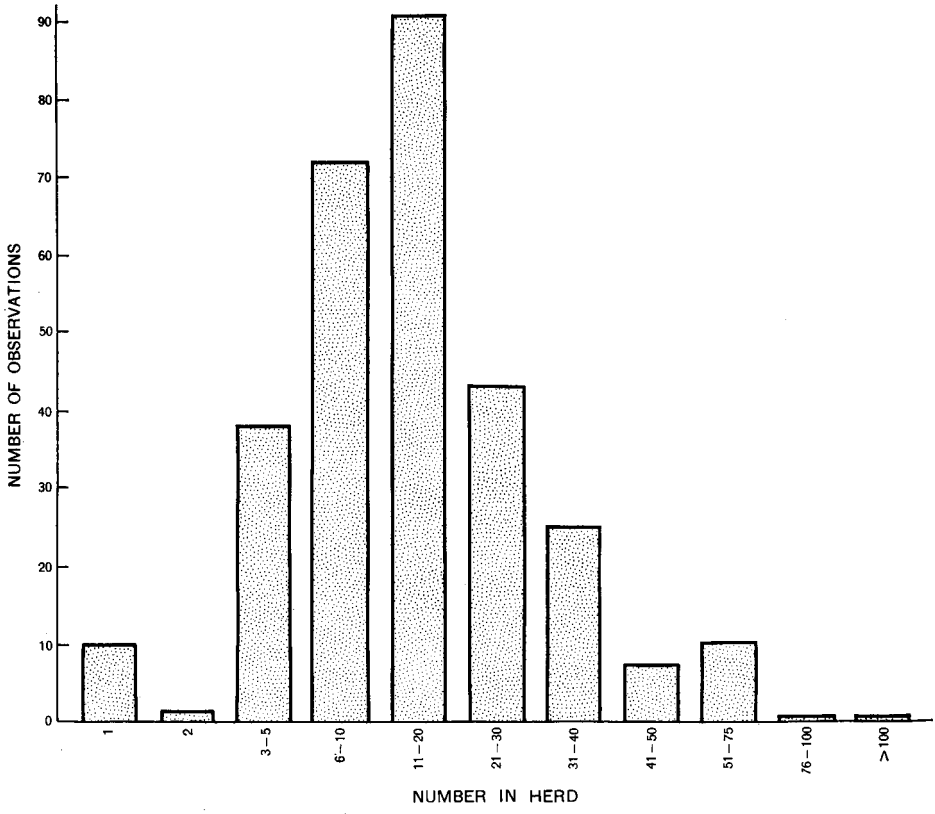

Fig. 4. Frequency of occurrence of mixed herds of various sizes in forested habitats.

but not in Fig. 5. It would also have the disadvantage of masking the scarcity of very small mixed herds (3-5), lone cows, and pairs (two cows or cow and calf).

Subject to this limitation, the data suggest the existence of a basic unit of about 11-20 individuals (possibly somewhat smaller in the forested habitat) with larger herds being formed by the transient amalgamation of two to many such basic units. This idea finds considerable support in the literature. Some authors, notably Seton (1929) went farther and believed, on the basis of purely circumstantial evidence, that the members of each unit, or clan, were blood relatives. Soper (1941) stated, without presenting any evidence, that "the various small herds and groups [of northern bison] are undoubtedly close blood relations". Garretson (1938) recognized that the large herds were formed by the close association of smaller groups, but did not believe that the smaller groups were either very stable, or blood relatives. McHugh (1958) was forced to conclude "that subgroup or group formation was flexible and depended little on blood relations beyond the age of 1 year". My data shed no light on the problem beyond pointing to the possible existence of a basic unit of some sort.

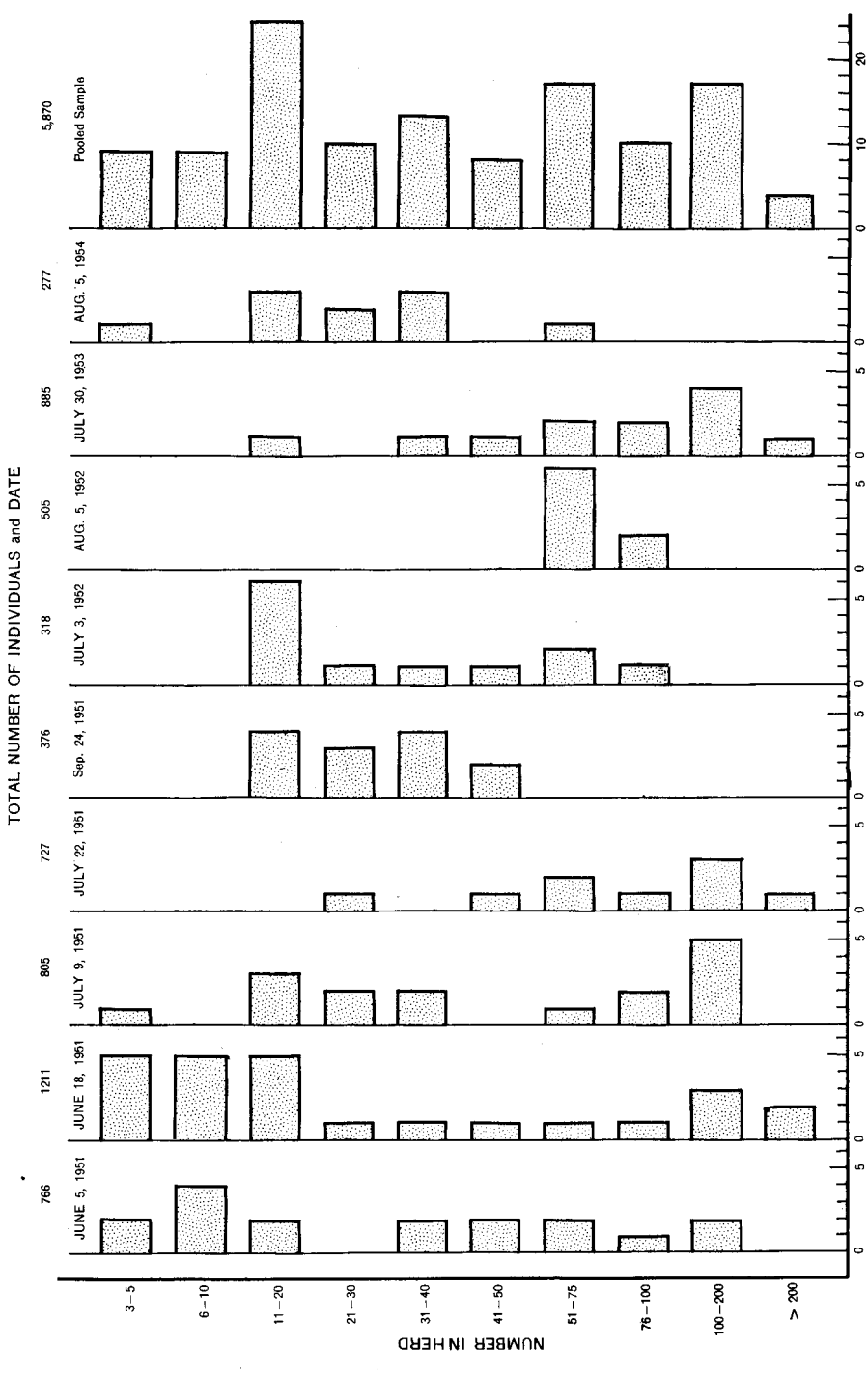

Fig. 5. Frequency of occurrence of mixed herds of various sizes on the Lake Claire meadows as observed from the air.

Intermingling of herds

In the discussion of herd size, it has been shown that there was much variation from time to time and from place to place. It is obvious, therefore, that there must be joining and splitting of groups to make larger or smaller herds. At least sometimes the union of two groups is accompanied by what amounts almost to a ceremony. This was observed three times in the field. The first observation was the most complete and will be described essentially as it was set down in my field notes for September 1, 1950.

I was stationed in the willow margin of a long narrow prairie watching a herd of 14 bison about 50 yards to my right. After about half an hour I noticed that the attention of this herd was being focussed more and more up the prairie to my left, and a few minutes later I heard bison vocalizing in that direction. Still later a herd of 18 bison emerged in single file from the timber bordering the prairie and began moving slowly toward the herd on my right. When the two herds were about 100 yards apart one bull advanced from each and the two met in a dry wallow directly in front of my position. They came toegther slowly, locked horns and pushed. This was a short encounter, without sharp impact and did not seem to be at all vicious. It ended as if by mutual agreement without any indication that one animal was victorious. The bull from the right herd then walked past his opposite number and joined the left herd, which had by this time advanced almost to the scene of the encounter. The bull from the left herd now led his group, which contained the bull from the right herd, to the end of the prairie where there was complete mingling of the animals from the two herds, without strife, but with much grunting. The bulls seemed uneasy, and walked stiffly with tails partly erect. In the next 30 minutes there was one short vicious battle between two bulls and a brief encounter between two cows. It was impossible to know the herd of origin of any of the combatants.

Two of the main elements of this incident seemed to be the preliminary meeting of two herd bulls, and the acceptance of an alien bull by one of the herds. These two elements were observed on each of the two subsequent occasions when two herds were seen to unite in this manner. The purpose seems to be recognition and the result is probably a minimum of strife when the two herds eventually coalesce.

No similar pattern was described by McHugh (1958) for any of the herds he studied, although he found that splitting and joining of groups occurred frequently. Perhaps his animals, which were confined to smaller ranges, had more frequent contact and thus recognized each other more readily.

Interspecific relations

Bison and wolves. The wolf is the only known predator of bison in Wood Buffalo National Park. In this section some observations of the behaviour of bison in the presence of wolves will be presented.

Bison appear to accept the presence of wolves without panic. I have noted this when watching herds from the air. On two occasions, our low-flying plane drove wolves from the midst of a large herd of bison. The wolves were not seen until they began to leave the herd. Nothing in the appearance or behaviour of the bison as we approached betrayed the presence of the wolves.

I have also witnessed wolf attacks from the air. On August 31, 1951, I observed seven wolves harassing a herd of nine bison, two of which were calves, on a large prairie along Murdock Creek. The bison were bunched closely together, so I was unable to tell the age and sex of the larger members. Several low passes with the plane drove away the wolves, but before we were out of sight they had resumed the attack. On my return the following day I was unable to find any sign that a kill had been made. Members of the park staff have reported similar incidents. The normal reaction of a herd caught thus in the open is to make a stand, closely bunched.

Individual bison caught in the open probably have little chance of beating off a wolf attack. The reaction of the bison in such an event is to attempt to reach the cover of heavy timber. This was noted in connection with each of four kills found during a wolf-control experiment carried out in the early winter of 1951-52. An unsuccessful attack was also recorded at this time (Fuller and Novakowski 1955). The bison probably seeks security in the forest because there he is able to dislodge any of his attackers that have secured a hold by rubbing or crushing them against the trees.

The wolves appear to single out one victim in a herd. This victim may be the subject of repeated attacks if the first attack is unsuccessful (Fuller 1957). Other members of the herd, with the exception of the mothers of calves under attack, show no regard for the presence of the wolves. The following incident, which took place on August 22, 1951, about 9 miles north of Pine Lake, illustrates this. On this occasion I stopped my truck when four bison, two bulls and two cows, appeared on the road ahead. They approached until the nearest, a cow, was standing on the right shoulder of the road only about 100 feet away (the distances were paced off later), and a bull was slightly behind her and on the left shoulder. The other pair stopped on opposite sides of the road about 100 feet behind the closer pair. Shortly after I stopped, a wolf appeared; and in the next 52 minutes a possible fourteen wolves (minimum of ten different animals) appeared in ones and twos either on the road or in the timber alongside the road. Each time a wolf appeared, the near cow, which I soon discovered had been previously wounded by wolves, became alert. Furthermore, with each slight breeze that I could see passing through the trees, she raised her head, or looked around. The other three bison were meanwhile lying down ruminating and took no notice of the wolves. The nearer of the two bulls never ceased ruminating during the entire incident as far as I could tell. At one point, 30 minutes after the first wolf was seen, a wolf peered

over the spoilbank bordering the road not more than 25 feet from the bull and cow farthest from me. Neither of these animals looked up. The wounded cow turned apprehensively to face that wolf. The bull nearest me (i.e., farthest from the wolf, also rose and turned, but showed no nervousness and in fact continued to ruminate. Probably the presence of my truck prevented the wolves from attacking. After they departed I shot the cow and found that she had previously been wounded by a bullet and had several tears on the thighs from an earlier wolf attack.

McHugh (1958) found that bison paid no attention to a female grizzly and three cubs that captured an elk calf within 700 feet of them. Goodwin (1939) and Soper (1941) noted indifference to wolves close to the herd. However, I know of no previous accounts of the behaviour of bison that were actually being stalked by wolves. Banfield (1954) noted a parallel situation among barren ground caribou *(Rangifer arcticus)* under attack by wolves. Far from exhibiting panic, some of the animals remained bedded down when the wolves passed as close as 50 yards away.

Reactions to man. The bison has been branded a mean and, at least occasionally, dangerous animal from early times down to the present. Thus Pennant (1793) says "The bison is very fierce and dangerous" and his illustration of a bull would convince even the most sceptical reader that this was true. Cahalane (1947) says "Normally the buffalo is a timid animal, but it is unpredictable . . . rarely the buffalo is bold and aggressive, but then it can be as dangerous as a rhinoceros". With this Soper (1941) is in essential agreement. He states, after describing an example of aggression towards his dog team: "Between the extremes exemplified in the ultra bold and the excessively timid, every conceivable shade of attitude and behaviour is displayed".

I have not found bison to be either aggressive or unpredictable at any time of the year. In mixed herds I have found them usually shy and timid. The bull groups may be "stupidly dull" as described by Soper, but I prefer to believe that their outstanding characteristic could be described as "stolid indifference" (Fig. 6). Likewise I have never been impressed by the curiosity of the northern bison. It certainly falls far short of the barren ground caribou in this respect.

There is a widespread belief among residents of Fort Smith who occasionally travel in the park that the bison are dangerous. Some people have reported that they were forced to stop their cars for an hour or more by a stubborn bull that disputed the right-of-way. Others will not venture into the bison range at all during August when the rut is at its height and the bison are supposed to be most aggressive. I have never encountered these stubborn bulls, nor have I observed increased aggressiveness toward people and cars during August. There is, at this time, however, more reluctance on the part of the bulls to give way. Even in August I was always able to dominate any bull I met although my English car weighed less than a full-grown bull.

Fig. 6. Bison bull in attitude of "stolid indifference".

During the course of this study I found myself in only two potentially dangerous situations. At 2245 on August 27, 1951, the truck that I was driving, a Dodge Power Wagon, was charged by a bull, which hit the bumper and left front fender with sufficient force to push the truck backwards up a slight incline. The animal then swerved away into the forest. I believe this animal was merely trying to escape and was blinded by the headlights of the truck that I had not had the presence of mind to extinguish. Had this not been so, the bull probably would have done additional damage to the truck. A more dangerous incident took place on August 10, 1951. D. R. Flook, Canadian Wildlife Service, and I were stalking a herd along the edge of a small meadow. We had passed some animals on the edge of the herd when we unexpectedly met a cow in the willows. When the cow wheeled and ran, a stampede for the timber was precipitated. We were in the line of retreat of six animals that had been feeding on the meadow. They came crashing through the willows directly for us but split into two groups of three and passed only 6 to 10 feet on either side of us when I shouted and waved my cap. Again, it is quite obvious that we were accidentally in the way and were not the victims of a premeditated attack.

References

Banfield, A. W. F. 1954. Preliminary investigation of the barren ground caribou. Canada, Wildl. Mgmt. Bull. Ser. 1, No. 10B, 112 pp.

Cahalane, Victor H. 1944. Buffalo go wild. Nat. Hist. 53:148-53.

————————1947. Mammals of North America. New York: Macmillan, 682 pp.

Fuller, W. A. 1957. The Biology and management of the bison of Wood Buffalo National Park. Ph.D. Thesis, unpublished, Univ. of Wis., 130 pp.

————————1959. The horns and teeth as indicators of age in bison. J. Wildl. Mgmt. 23:342-44.

Fuller, W. A. and N. S. Novakowski. 1955. Wolf control operations, Wood Buffalo National Park, 1951-52. Canada, Wildl. Mgmt. Bull. Ser. 1, No. 11, 20 pp.

Garretson, M. S. 1938. The American bison. New York: New York Zoological Society, 254 pp.

Goodwin, George G. 1935. Buffalo hunt. Nat. Hist. 36:156-64.

————————1939. The bison. *In* Ely, et. al., North American big game. A book of the Boone & Crockett Club. New York: Charles Scribners Sons, pp. 359-370.

Grinnell, G. B. 1904. The bison. *In* Musk-ox, bison, sheep and goats. New York and London: Macmillan, 284 pp.

Hornaday, W. T. 1889. The extermination of the American bison, with a sketch of its discovery and life history. Washington: Smithsonian Report, 1887, pt. 2:367-548.

————————1922. Minds and manners of wild animals. New York: Charles Scribner's Sons, 328 pp.

McHugh, T. C. 1958. Social behaviour of the American buffalo *(Bison bison bison)*. Zoologica 43:1-40.

Pennant, T. 1793. History of quadrupeds. 3rd Edition. London: B. & J. White, Vol 1, 306 pp.

Roe, F. G. 1951. The North American buffalo. Toronto: University of Toronto Press, 957 pp.

Scott, J. P. 1958. Animal behavior. Chicago: University of Chicago Press, 281 pp.

Seibert, F. V. 1925. Some notes on Canada's so-called wood buffalo. Can. Field-Nat. 39:204-6.

Seton, E. T. 1929. The buffalo. Lives of game animals. New York: Doubleday, Doran and Co., Vol. 3., Pt. 2:639-717.

Soper, J. Dewey. 1941. History, range and home life of the northern bison. Ecol. Monogr. 11:347-412.