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American bison behavior patterns at

Wind Cave National Park

by

Milo Jack Shult

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of

The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Zoology and Entomology Major: Wildlife Biology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

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For the Graduate College

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#### INTRODUCTION

Authors have been writing about the North American bison (<u>Bison</u> <u>bison bison</u>) since the Spanish explorers first saw the animals. Rorabacher (1970) reportedly examined more than 900 titles while preparing his book on the bison. This extensive literature on the history of the bison contains many references to the behavior of the creature. However, much of the information is based on generalizations of legends and secondhand observations. Roe (1951) documents the contradictory nature of the references to bison behavior from earlier literature in his chapters five, six, and seven.

Catlin (1841) is one of the few early workers who viewed the bison with the eye of a trained observer. Hornaday (1889) originally published a somewhat contradictory discussion of bison behavior but in a later book (1922) presented an analysis based on more factual observation. Seton (1929) and Garretson (1938) both presented some accurate material on bison behavior, although Seton's work is also flavored with the acceptance of doubtful statements from earlier publications.

Six recent works either make references to or deal in detail with bison behavior. Soper (1941) makes many references to bison behavior in his published account of a 2-year study in Canada. McHugh (1958) provides one of the most complete descriptions of bison behavior based on observations of 3 bison herds with additional data gathered from 6 other herds, all in the United States. Fuller (1960) bases his publication on observations of behavior made during a study from 1950 to 1956 on the biology of bison in Wood Buffalo National Park with particular reference to the

effects of tuberculosis on that herd. Egerton's work (1962) deals with cow-calf relationships and rutting behavior as observed primarily in a small captive herd in Waterton Lakes National Park, Alberta. Engelhard (1970) worked with calf behavior during the spring and summer of 1967 in Montana. Maegher (1970), in describing the past and present status of the bison of Yellowstone National Park, provides additional information on the behavior of that herd.

Preliminary studies of bison behavior were begun by the Iowa Cooperative Wildlife Research Unit in 1966 when an undergraduate NSF student spent the summer months at Theodore Roosevelt National Memorial Park in North Dakota studying bull bison. Another NSF undergraduate worked in the summer of 1967 at Theodore Roosevelt and at Ft. Niobrara National Wildlife Refuge in Nebraska. The Ft. Niobrara study was continued in the summer of 1968, again by an NSF undergraduate.

On June 1, 1968, field work was begun for a Ph.D. program at Wind Cave National Park in South Dakota. That field period was terminated November 17, 1968. A second field study period started March 10, 1969 and finished February 24, 1970. The bison behavior studied during these periods provides the basis for this dissertation.

In addition to the Ph.D. program, an M.S. student worked at Wind Cave during the summer of 1969 and the summer and fall of 1970. This portion of the study again dealt primarily with bull behavior.

The main emphasis in my study was placed on calving behavior, cowcalf relationships, and rutting behavior. However, observations of bison behavior were made throughout the year to provide a basis for comparison

with the calving and rutting periods. The study was designed with three main goals.

The first goal was to add to the increasing knowledge of the natural history of the bison. As has already been indicated, many of the earlier writings on the bison either do not discuss or do not deal factually with the habits of this species. Until 1958 the main scientific bison studies dealt with disease control, aging, and hybridization.

Secondly, it was believed that this study and others like it may be of particular use to anthropologists studying the American Indian, especially the tribes of the Great Plains. Haynes (1970) summarizes the degree of dependence of these peoples on the bison. It must be pointed out, however, that care must be taken in directly correlating the behavior patterns of bison studied today with the early historic and prehistoric herds. Bison once roamed over most of the United States, Canada, and parts of Mexico in numbers generally estimated at 60 million (Hornaday 1889). Today approximately 17,000 bison can be found in the United States with probably an equal number in Canada (Rorabacher 1970). These animals are found in herds of varying size primarily on enclosed areas. It is very possible that changes in behavior have taken place from the time of the vast herds. This is one of the reasons that calving and rutting behavior was selected for emphasis in this study. It is quite probable that the ritualized behavior patterns of calving and courtship are the least changed.

Finally, the third goal of the study was to provide and make available information which will increase the recreation potential of the bison.

Because many of the animals today are located on parks and refuges, it was believed that visitors to these areas will enjoy better outdoor experiences if they have a better knowledge and appreciation of the animals they are watching. With visitation to these areas being the greatest during the summer months, it is important that the patterns of calving and rutting behavior of this period be made available.

### THE STUDY AREA

Wind Cave National Park, South Dakota's first and only national park, was established by an Act of Congress and the bill signed by President Theodore Roosevelt on January 9, 1903. Wind Cave is the seventh national park in the United States. The park was established to preserve the extensive limestone cavern from which it draws its name. This is the only cave in the world where a colorful crystalline calcite formation known as "boxwork" occurs in such abundance (Soil Conservation Service 1969).

The original boundary included approximately 10,560 acres, of which only part is included in the park today (Fig. 1). On March 4, 1931 the boundary was extended to include Beaver Creek canyon and two springs near where Norbeck Lake is located today. This extension brought the total acreage in the park to 11,718. In 1946 President Harry Truman approved the present boundary which increased the size of the park to 28,059 acres (Bohi 1962). The south boundary of the park is 6 miles north of Hot Springs, South Dakota. The north boundary is shared with Custer State Park which has a bison herd of approximately 2000 animals.

Wind Cave is located in the southern Black Hills and represents a transition zone or ecotone between the coniferous forest and grasslands of South Dakota. The park consists of hills, valleys, canyons, ridges, and mesas with interspersed stands of ponderosa pine (Pinus ponderosa) and grassland. Predominant grass species on the area include big bluestem (Andropogon gerardii), little bluestem (Andropogon scoparius), western wheatgrass (Agropyron smithii), needlegrass (Aristida sp.), needle and thread grass (Stipa comata), blue grama (Bouteloua gracilis), hairy grama

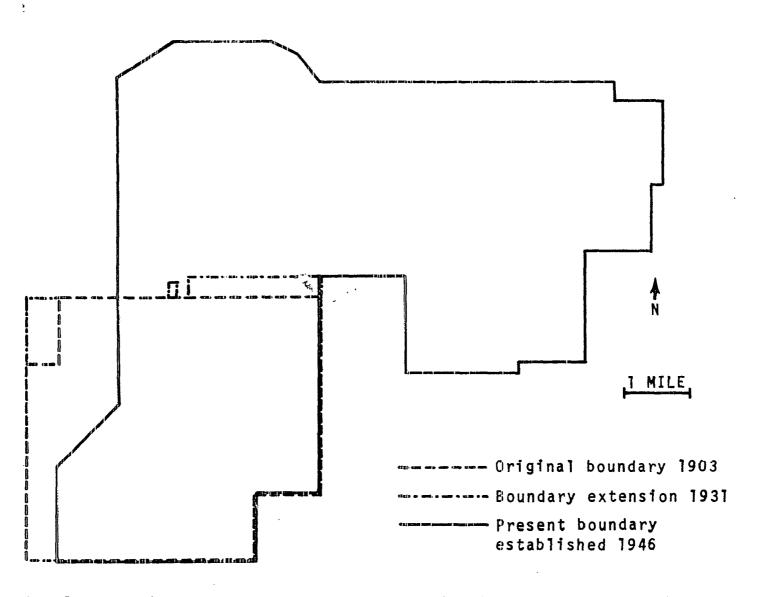


Fig. 1. Boundary changes at Wind Cave National Park from establishment in 1903 to the present

(<u>Bouteloua hirsuta</u>), side-oats grama (<u>Bouteloua curtipendula</u>) and buffalo grass (<u>Buchloe dactyloides</u>) (Soil Conservation Service 1969, Pohl 1968). Forbs and woody browse species also occur mainly on specific site types.

Vehicle access for visitors to the park is limited to 18 miles of paved highway and 9 miles of secondary gravel road (Fig. 2). In addition there are 28 miles of trails for use by authorized personnel only. These trails are designed to provide access to more remote areas of the park for fire suppression. Except when weather conditions make these trails impassable, they can be travelled in two-wheel drive vehicles with adequate frame clearance, such as pick-ups.

The park is enclosed with 34 miles of boundary fence primarily designed to prevent bison from leaving the area. The fence consists of 8-foot high woven wire except on a portion along the west boundary which is 5 feet high. This latter portion was designed to permit elk (<u>Cervus</u> <u>canadensis</u>) to move between the park and the Black Hills National Forest. Autogates (cattle guards) designed to allow vehicles to enter or leave the park but to discourage bison movements are located at the six entrances where primary and secondary roads come into the park. Fire trails which leave the park are blocked by locked woven wire gates.

Visitation to the park between 1965 and 1971 has shown some fluctuation but indicates an increase in total visits from 885,643 in 1965 to 1,085,297 in 1971 (Fig. 3). These figures are based on calendar year totals from December Monthly Public Use Reports (Form 10-157) for each year.

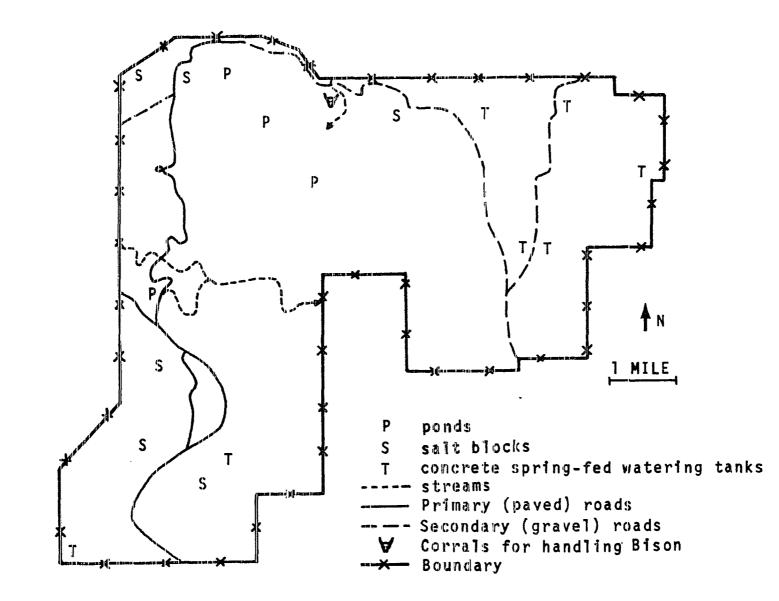


Fig. 2. Man-made features and natural streams at Wind Cave National Park

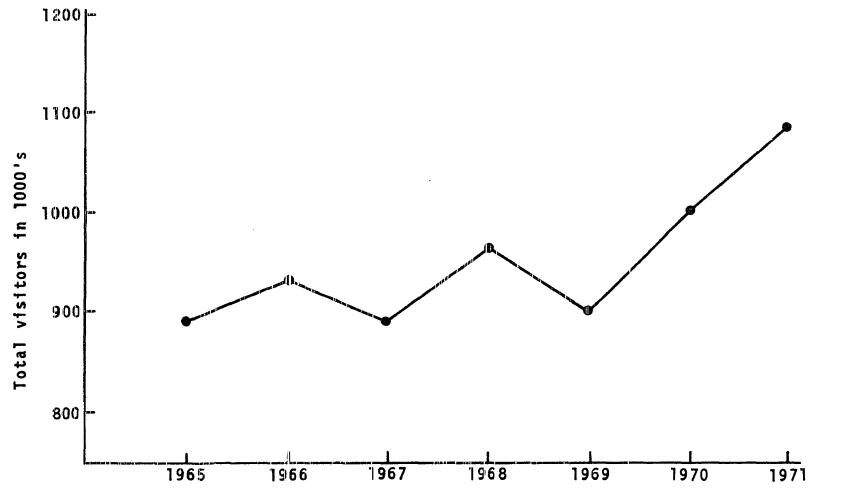


Fig. 3. Numbers of visitors to Wind Cave National Park 1965-1971

#### THE BISON HERD AND ITS MANAGEMENT

Bohi (1962), in his work describing 75 years at Wind Cave, provides an interesting background of the bison herd. According to his narrative and other sources, bison were first introduced at Wind Cave on November 28, 1913. This introduction was made possible primarily through the efforts of the then active American Bison Society. Fourteen bison were brought to the area from the captive herd of the New York Zoological Society. Garretson (1938) describes the herd as consisting of 7 males and 7 females.

By 1915 the nucleus herd had increased to 16 animals. In that year 2 males and 4 females were brought in from Yellowstone National Park. By 1918 the herd totaled 42 animals.

In February of 1936 the first bison roundup was held. The herd at that time totaled 171. Also in that year a bull named "Old Sandy" died. Apparently this bull was part of the original group introduced on the park. Because of his light coloration and "leadership" qualities he was well known to the park personnel. The bull was 24 years old when he died.

In October of 1938 the bison roundup showed a total of 288 head. In that year 64 animals were shipped to the Pine Ridge Indian Reservation, also in South Dakota, to increase the herd there. Bohi's next reference to the bison lists 431 animals counted on the park in 1955.

In the 1960's the National Park Service initiated a program to eradicate brucellosis from the bison herd. Brucellosis or "Bang's disease" is a bacterial disease produced by organisms in the <u>Brucella</u> group. In cattle it quite commonly causes spontaneous abortion. When brucellosis

infects bison bulls, the testes may become enlarged and abcessed. In bison cows the bacteria affect the supramammary lymph nodes, and uterine abcesses may cause abortions in initial infections. Rorabacher (1970) indicates that brucellosis is not serious in bison as the animals adapt to the disease a year after the initial infection and further symptoms are rare. In 1965 Wind Cave began rounding up bison to vaccinate heifer calves against the disease and to test the herd.

Participation in the roundups of 1968 and 1969 provided the data necessary to construct the age and sex structure of the herd during the study period. In 1968 a total of 276 bison were handled in the roundup (Table 1). Approximately 25 bulls were not captured in the roundup bringing the total number of bison on the study area to 301.

	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		Calves		<u></u>
	Bulls	Cows	Male	Female	Total
Total captured	97	116	36	27	276
Total culled	38	23	0	1	62
Totals remaining in herd	59	93	36	26	214

Table 1. Number and sex of bison handled and culled in the 1968 Wind Cave National Park roundup

Examination of the card file on bison at the park indicated that the maximum overwintering population was 241. The sex and age distributions of these animals are shown in Figure 4 as they appeared after the 1969 calving season.

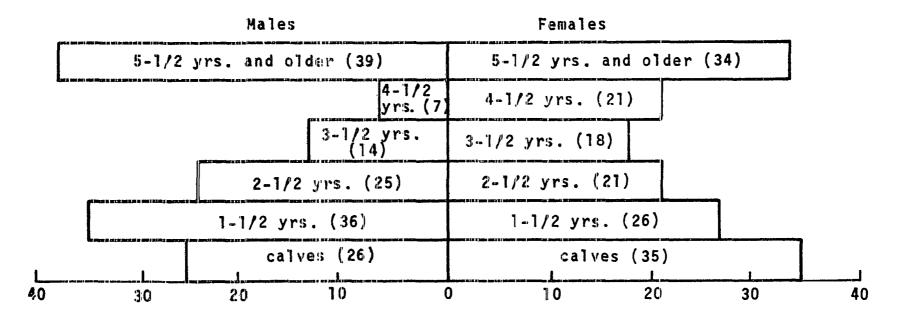


Fig. 4. Age and sex distribution of Bison at Wind Cave National Park following the 1969 calving season based on the results of the 1968 roundup

In 1969 bison were rounded up as part of the brucellosis eradication program. An attempt was made to immobilize animals not corralled. Further attempts were made to shoot all animals on the park not tested either in the corrals or by the immobilization crew. A total of 274 bison were handled in these operations (Table 2). Of that number 52 were culled leaving a total of 222 animals. Figure 5 shows the sex and age distributions of those animals.

			Calves		
	Bulls	Cows	Male	Female	Total
Total captured	101	112	26	35	274
Total culled	28	22	1	1	52
Totals remaining in herd	73	90	25	34	222

Table 2. Number and sex of bison handled and culled in the 1969 Wind Cave National Park roundup

All bison which show possible positive reactions, including weak reactions to the brucellosis test are culled. Some animals are also removed to keep the herd at the desired population level and natural sex and age ratios. All culls are turned over to the Bureau of Indian Affairs and are then butchered and the meat used on the Sioux Indian reservations. Rorabacher (1970) states that, as far as is known, brucellosis does not, in any way, affect the quality of the meat to the extent that it would be inedible.

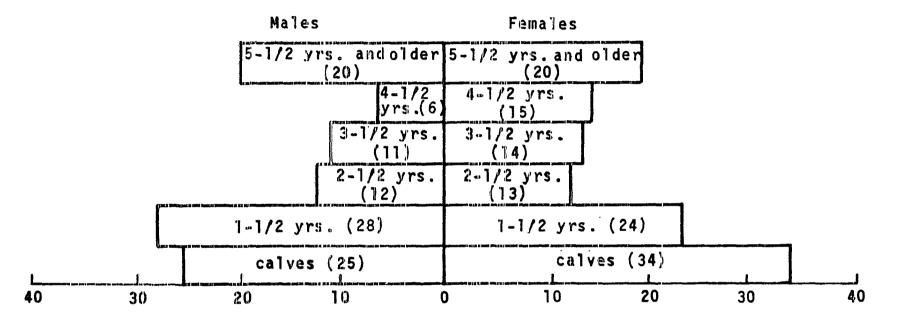


Fig. 5. Age and sex distribution of Bison at Wind Cave National Park following the 1969 roundup and cull

With the exceptions of the roundup and the occasional destruction of crippled animals, no other management practice requiring handling or harassing the animals was used.

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#### METHODS

My wife and I lived on the area in park housing throughout the field portion of the study. For transportation, a two-wheel-drive carry-all van with a four-speed transmission was used. This vehicle was used on the primary and secondary roads and along fire trails to locate the bison. When the bison were in locations where they could be approached and observed from the vehicle, the van proved to be an excellent blind which rarely disturbed the bison in the manner a man on foot or rider on horseback would. Engelhard (1970) also found a vehicle preferable as a means of approaching bison as compared with a man walking erect or riding erect on horseback.

In late spring of 1969 a horse was purchased for use during the remainder of the study. While the horse posed some problem in transportation of equipment and decreased success in approaching the bison directly, it was very useful for covering areas where a vehicle could not travel and for locating bison in these areas. When neither the vehicle nor the horse was practical I hiked over remote areas of the park and stalked the bison on foot. This was an excellent means of observing the animals as long as the investigator was not discovered but had the disadvantage of severely limiting the territory which could be covered in a day.

Daily activities of the bison were recorded throughout the study period. Random observations were made for all hours of the day and night using a portable cassette-loading tape recorder for field notes. The recorder permitted continual observation of the animals without looking away to make written notes and thereby losing continuity of observation.

Field notes were then transcribed into bound journals.

During the study a total of 3,363 recorded observations were made of bison activities during a total of 2,929 hours in the field searching for and observing the animals (Appendix Table 1). Recorded observations documented time of day, location, age, sex, group type (cow-calf or bull), habitat, and activity. Bull groups are defined as those which contained only males and include observations of bulls ranging alone. Cow-calf groups are those which contain cows, calves (including animals approaching one year of age during the winter and early spring), and any bulls that might be in with them. This includes groups with older bulls present during the rut as the nature of these groups remained essentially matriarchal. McHugh (1958) used essentially the same classification of group types. During the study observations were made on 346 cow-calf groups and 896 bull groups. Obviously these numbers do not represent total individual numbers of such groups on the area but rather totals of daily observations of individual groups. Observations include instantaneous observations of animals made during surveys of the area and prolonged series of observations on individual groups.

In addition to the recorded observations, experience was gained in observing bison during times when detailed field notes were not taken. This includes such times as participation in the annual roundup and culling activities. It also includes general observations made while butchering road kills or destroying crippled animals. Horseback riding and hiking for pleasure on the area also added to this experience.

In addition to field notes, behavior patterns were recorded on film

using a 35mm single lens reflex camera with 55mm and 300mm lenses, and a Bell and Howell Super 8 movie camera with a zoom lens adjustable from wide-angle to telephoto. Over 500 color 35mm slides were taken on the area and approximately 150 black-and-white photos. A total of 1050 feet of movie film was taken and used in analysis of behavior patterns and movements. Other slides and movie film from other project personnel were also available for analysis.

During the summer and fall of 1969 a time-lapse movie camera device was placed overlooking one of the water holes on the area. The apparatus was designed to expose one frame of Super 8 film every 5 minutes during daylight hours. The camera was visited periodically to mark date and time for frames of reference. A total of 97 days of activity was recorded for this water hole in this manner.

The Conservation Plan for Wind Cave National Park describes six types of range sites and three types of woodland sites based on soil types, topography, and vegetation (Soil Conservation Service 1969). Bison were observed in all of these types during the study. The three woodland sites were consolidated and will be discussed simply as woodlands. The range sites will be called grasslands and prairie dog towns. During the study there were eight active towns of blacktail prairie dog (<u>Cynomys 1</u>. ludovicianus) on the area which were visited by the bison.

Excluding the fenced campground and headquarters area, a total of 27,583 acres of the 28,059 acres was available to the bison. The prairie dog towns collectively accounted for 904 acres (3.2%) of the area. Woodlands accounted for 4,917 acres (17.6%) of the area and the remaining

grasslands totaled 22,176 acres (79.2%) of the area. These figures are based on the Conservation Plan map and the percentages of woodlandgrassland interspersion presented therein (Soil Conservation Service 1969). The acreages for the prairie dog towns are based on area within outside perimeter points observed during the study. Figure 6 shows the distribution and relative size of those towns.

Due to the broken terrain on the area, bison were often located from a high point with the aid of 7 x 50 binoculars and a 20x spotting scope mounted on a rifle stock. When animals were sighted, the method of approach was dictated by the terrain of their location. As my experience on the area increased, the animals could be spotted at long distances without the aid of binoculars or scope, although these were valuable in recording behavior activities. Most observations of cow-calf relationships and courtship behavior took place at distances less than 100 yards.

Radio telemetry was first used in the study in 1968 when 10 radio transmitters were attached to 9 bulls and 1 cow. The transmitters were in the range of 150 mc. frequency and were attached to a collar of rubberized belting fitted around the neck of the animals. Eight of the bulls were immobilized using the drug M99. Drug action was reversed with injections of M285. One of the bulls and the cow were handled while in a squeeze chute during the roundup. Due to electronic problems the data from these animals in 1968 is limited. Southern (1965) points out that equipment problems are not uncommon when telemetry devices are first used on a species. In 1969 many of the problems with the equipment were solved and 14 more transmitters were attached to new bulls or used to replace

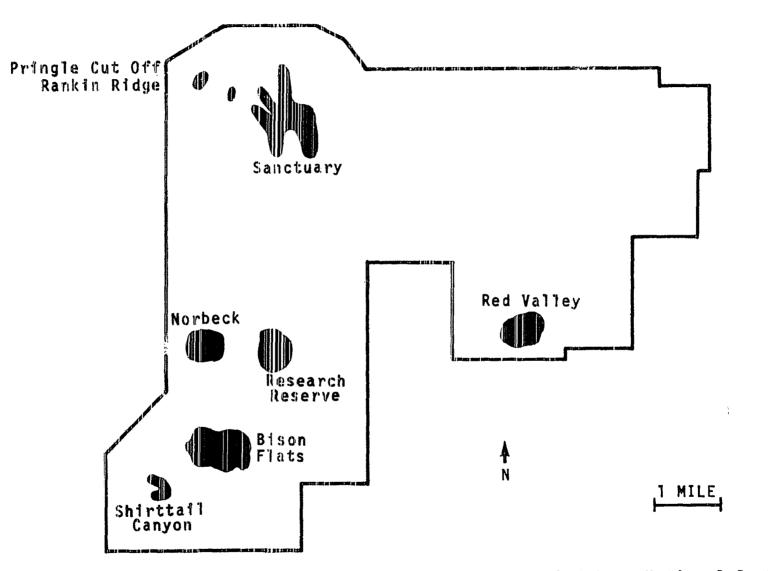


Fig. 6. Names and distribution of prairie dog towns on Wind Cave National Park during the study period

faulty ones on previously tagged animals.

Although information from the tagged bulls is used in this study, the data of greatest importance here were obtained from the cow tagged in 1968. The animal was an adult female captured in the roundup. During handling operations the animal was extremely troublesome and was tagged to determine the extent of her leadership influence in the herd. Although the transmitter stopped functioning between April 22 and April 30, 1969, the collar was used to positively identify the animal until lost in the handling procedure in the 1969 roundup. The cow gave birth to a calf in 1969 and provided much information on cow-calf relationships.

In addition to the drugs already mentioned, M50-50 was used as an antagonist to M99 in 1969. Throughout the bison project, Iowa Cooperative Wildlife Research personnel have attempted 65 immobilizations. These include early experiments with the drugs, attachment of radio transmitters, and collection of blood samples for brucellosis testing. The results of these immobilization attempts are presently being analyzed but will not be discussed here.

Besides observations on specific individual activities, general behavior during the entire day was recorded. McHugh (1958) termed this the daily round and divided it into two main types of activity--feeding behavior and non-feeding. In this study the daily round is broken down into four categories. These are grazing, watering, moving (i.e. changing

locations while not grazing), and loafing (such as lying or standing and ruminating). The total observations for these categories are presented in Appendix Table 2.

Aging of bison during behavior observations necessitated use of gross anatomical characteristics. Hornaday (1889) first described field methods of estimating ages of bison and his techniques were expanded by McHugh (1958) and Fuller (1959). The main criterion in estimating age was based on size, shape, and wear of horns. Bulls were aged accurately up to 5 or 6 years and approximately up to about 14 years. Cows were aged accurately up to 3 years with approximations up to about 9 years. In addition to horn characterístics, relative size of the animals and amounts of hair on the head and forelegs were useful criteria. Ages of calves during the first 4 months were based on observed increases in size and changes in pelage coloration from the typical reddish-brown or tawny hues of the newborn animals to the characteristic dark brown of the adults.

McHugh (1958) cites Pope's (1919) method of estimating age in cattle by development and subsequent wear of permanent incisor teeth on the lower jaw and states that this method may be used favorably with bison. In this method, age up to and including 5 years may be estimated by the appearance of each pair of incisors. Beyond 5 years age is approximated by leveling or wear in the incisors. Novakowski (1965) also discusses incisor wear as an indicator of age using cemental deposition as a standard. During this study experience in aging bison was enhanced by examining incisor replacement in animals handled during the roundups.

As some animals were of known age from ear tag numbers of previous handlings, observations of these bison during the roundup increased the accuracy of field aging techniques.

During the culling operations following the roundup, reproductive tracts were collected from cows removed from the herd. Tracts were also collected in 1969 from cows culled from the Custer State Park herd. These tracts were taken to Iowa State University and added to a collection of bison tracts from other years and other areas. Data on the presence or absence of corpora lutea, presence or absence of embryos in the uterus, and embryo development are presently being analyzed to contribute information to the breeding biology of the bison. In addition, testes were collected from 21 bull bison culled in 1968 and fresh smears were made from the epididymis of each one. These smears were examined with the aid of a microscope to determine the relative abundance of sperm. Fuller (1961) made similar examinations on testes from 20 young male bison at Wood Buffalo National Park. A comparison of the results from this study with those of Fuller will be made in the discussion of breeding behavior.

# RESULTS AND DISCUSSION

A major goal in the study of animal behavior must be objectivity in observation and report of observations (Fraser 1968:3). However, it must be recognized that complete objectivity is never possible. In fact, concentrated effort to completely avoid subjectivity may prove to be deceiving (Spurway 1956). A presentation of numbers and mathematical manipulations may be as misleading as the presentation of nothing but anecdotal accounts of behavior. While individual observations should be as objectively descriptive as possible, presentation of the results of a behavior study may require categories of behavior patterns based on expected results from previous studies, seasonal variation in behavior, and presentation of atypical observations which deviate from the normal. Scott (1958) presents nine categories of adaptive behavior. These will be used in this paper with modifications where appropriate.

### Herd Organization

Early writers recognized a separation of bison groups by sexes, particularly the habit of bulls ranging alone. This was thought by many to be the result of defeat of a bull in combat and exile from a herd. Even General George A. Custer described the "driving away of a hated antagonist" from the herd (Custer 1962:14). Recent works have shown this separation to be a behavioral characteristic of the animal rather than evidence of conquests.

McHugh (1958:14) classified bison into bull groups and cow groups according to composition. Fuller (1960:10) preferred the terms mixed

group and cow groups for the northern bison because these herds nearly always contained some mature males as well as mature females and young of both sexes. Engelhard (1970:17-18) used the terms bull groups and cow groups. Maegher (1970) used the terminology mixed herd groups, bull groups, and solitary bulls. Egerton (1962:8) does not make the distinction between groups as the Waterton Herd where she concentrated her study consisted of 25 animals which generally behaved as a unit. These animals were confined to an enclosure under three-quarters of a section in area and divided into a winter pasture of a little less than a quarter-section and a summer pasture of a half-section.

In this paper the terms cow-calf groups, bull groups, and lone bulls will be used. Bull groups include only those groups made up entirely of males. Lone bulls are males observed ranging alone at any given time. Cow-calf groups are those with cows and calves present. These groups also had yearlings of both sexes and bulls up to 3 years of age in them. Due to similarities in leadership and habits, the groupings of the rutting season are included in the cow-calf category even though adult bulls moved into these groups during that season. The groups observed during the rut will be discussed in detail later in the paper.

# Bull groups and lone bulls

Bull groups varied in size from 2 to 17 animals and consisted of bulls 4-years old and older. Frequency of occurrence of lone bulls and bull groups of various sizes are presented in Fig. 7. Lone bulls accounted for 525 (58.6%) of 896 observations of bull groupings. This figure is somewhat biased due to duplication of observations. However, as the

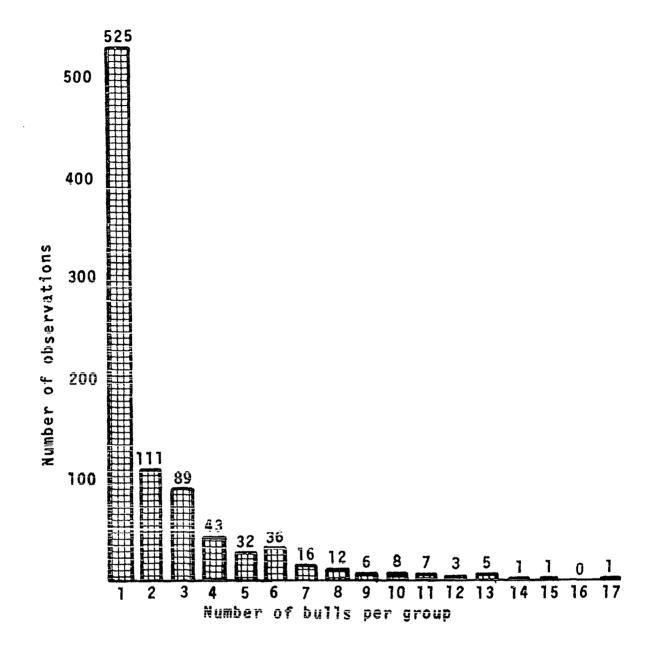


Fig. 7. Frequency of occurrence of lone bulls and bull groups of various sizes at Wind Cave National Park

observations are based on daily totals which were not duplicated (i.e. bulls observed on the same day in the same location are not included) the figure clearly indicates that chances of observations of bulls ranging alone are much higher than for groups of two or more animals. Fuller (1960:11) found comparable results from road counts in Wood Buffalo National Park which yielded 488 lone bulls, 88 groups of two, 49 groups of 3 to 5, and only 9 groups of 6 to 10. His lower numbers of groups over 5 as compared to that observed at Wind Cave is probably due to the forested habitat where he made his counts.

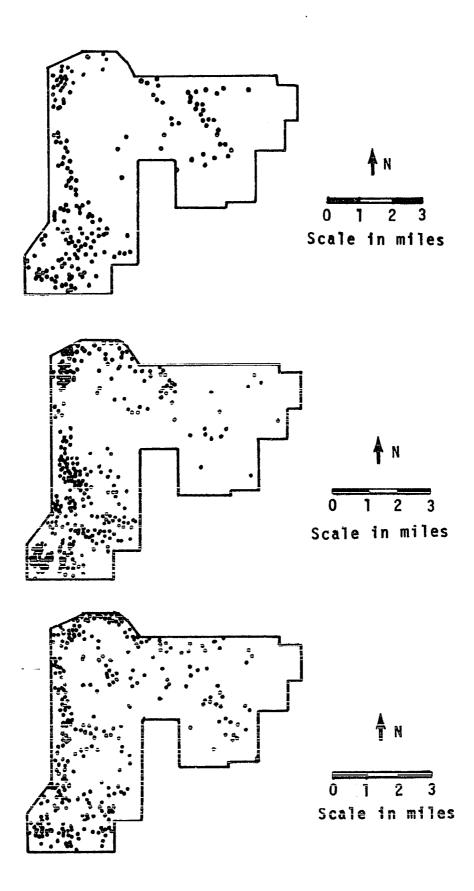
Lone bulls and bull groups were observed in all parts of the park throughout the study period but were especially concentrated in the southwest portion. Figure 8 illustrates the distribution of these groups during 1968 and 1969 excluding the breeding and calving seasons. During the calving seasons of both years (April through June) lone bulls and bull groups continued to inhabit the southwest portion of the park in high concentrations but began to move northward in June prior to the rut (Fig. 9). During the rut (July through September) the lone bulls and bull groups observed were more frequently in the central and eastern part of the park in the vicinity of the cow-calf groups but moved back into the southwest portion during September as breeding activity declined (Fig. 10).

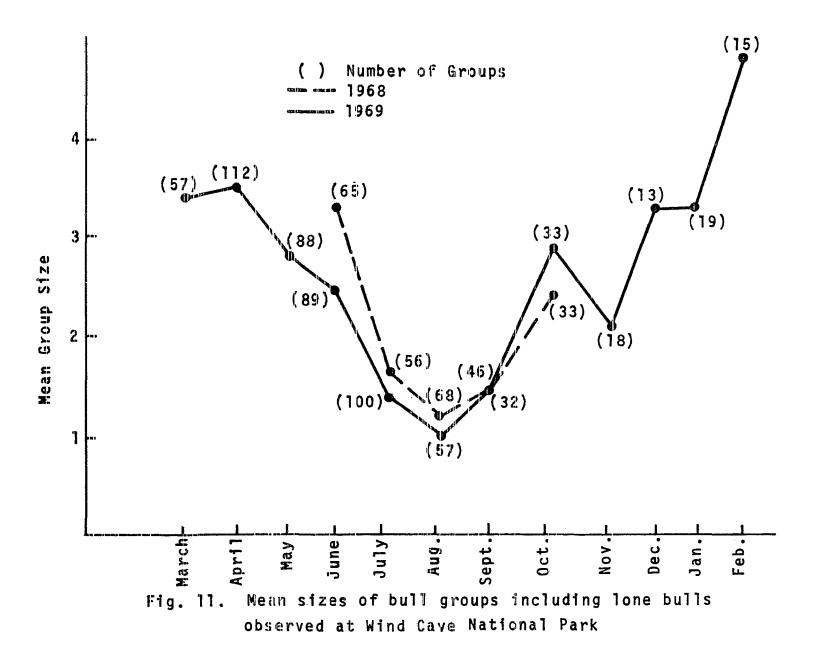
Sizes of bull groups varied throughout the year. Lone bulls are included in the analysis of group sizes to best demonstrate this variance. Group size averages were largest during the non-breeding portion of the year (Fig. 11). Prior to the rut, group sizes dropped from a mean of 2.8 in May to 2.5 in June (both figures for 1969). These figures compare

Fig. 8. Distribution of lone bulls and bull groups at Wind Cave National Park for October 1968, March 1969, and October 1969 through February 1970. This represents distribution throughout the year with the exceptions of the calving and breeding seasons

Fig. 9. Distribution of lone bulls and bull groups at Wind Cave National Park for June 1968 and April - June 1969. This represents the distribution during the calving seasons

Fig. 10. Distribution of lone bulls and bull groups at Wind Cave National Park for July - September of 1968 and 1969. This represents the distribution during the rut





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favorably with the mean group size of 2.4 observed by McHugh (1958:15) at Wind Cave in May 1952. During August of 1968 and 1969, the peak of the rut for both years, the mean group sizes were 1.0 and 1.2 respectively. McHugh (1958:15) also observed a mean size of 1.2 during the rut in the Hayden Valley herd in Yellowstone National Park. These decreases in group sizes prior to and during the rut undoubtedly are reflections of bulls moving into the cow-calf groups and decreased tolerance among bulls during that time. As bulls dropped out of the cow-calf groups following the rut, sizes of groups again increased in both years of the study.

Group integrity in bull groups was not as well defined as in cowcalf groups. Sizes of groups and individual members recognized by physical characteristics often varied from day to day. The longest period of association noted in the study was 9 days in October of 1969 when two individuals remained together. One of the bulls was marked with a radio transmitter (Channel 6) and the other was identified by a hip tag (number 640) put on during the roundup of that fail. Both bulls were estimated at 10 years of age. Another group of 10 bulls remained together for two and one-half days during that same month although it is not known if the same individuals were together each day.

McHugh (1958:15) comments that older bulls tend to lead bull groups more often than younger ones, but there is great variation. This same statement is true at Wind Cave. Leadership in bull groups was limited primarily to allelomimetic (contagious) grazing behavior and to moving from one location to another without grazing. Even these patterns showed

wide variation. As example, 22 observations were made on the activities of the Channel 6 and number 640 bulls previously mentioned. During 9 of those observations the bulls were observed behaving differently (i.e. one grazing and the other lying down). During the observations when the bulls were engaged in the same activity, Channel 6 was observed to initiate the activity 5 times with the remaining 8 times initiated by the other bull.

Bull groups generally moved from one area to another by traveling in a single file. Distances between members varied from 10 yards up to onequarter mile. The intervals varied with the time delay for members of a group to imitate the behavior of another member wandering off. Both moving and grazing activities appeared more easily imitated by members of a group at dawn and dusk.

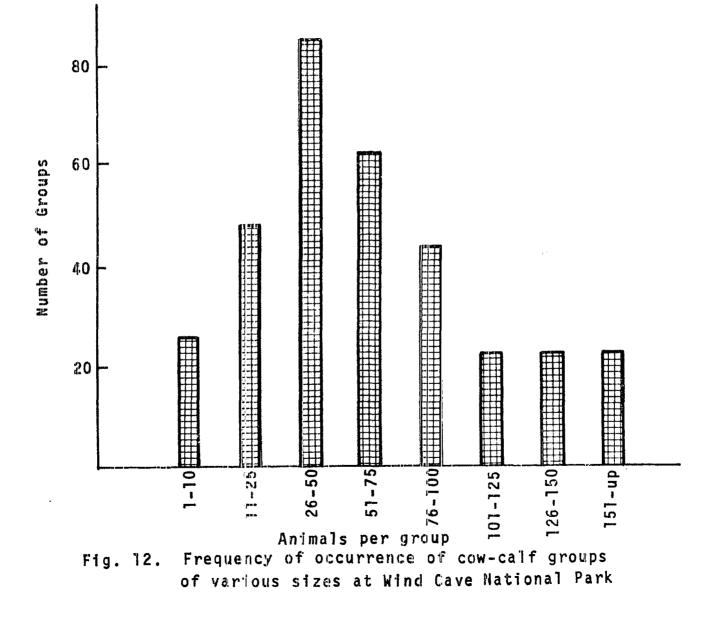
Lone bulls and bull groups were much less wary of human approach than cow-calf groups (except during the rut). Flight distance for bulls was usually under 100 yards, and on one occasion I accidently approached within 10 feet of a bull before it stood up and then stared at me. Even when approached closely, bulls usually just wandered off rather than running away. This was not true following the roundup or after periods of immobilization if the animals were harassed. However, such disturbance activities are unusual and the resultant behavior is not representative of the activities of undisturbed bison. Bulls could be made to run away by sudden moves in their direction or by tossing rocks at them, but these methods were seldom used as it interfered with normal behavior cbservations.

Habitat preference for lone bulls and bull groups was based on 1022 observations (Appendix Table 3). Of that number 733 (71.7%) were made in grasslands, 103 (10.1%) in prairie dog towns, and 186 (19.2%) in woodlands. These figures suggest that grasslands were the most heavily used habitat type. However, there also appeared to be a seasonal preference for prairie dog towns and woodlands. Forty-seven of 86 (55.8%) of the prairie dog town observations and 76 of 131 (58.0%) of the woodland observations occurred during May-August in 1969. This period represents the times of shedding of the winter coat of hair from the back half of the animals' bodies and the occurrence of hot weather (Appendix Fig. 1). The prairie dog towns and woodlands were used to a greater extent during these times for wallowing, loafing, and rubbing activities (these activities will be discussed later).

## Cow-calf groups

Cow-calf groups were more complex in their structure than bull groups. During the non-breeding seasons of the year these groups consisted of cows of all ages, calves and bulls 3 years old and younger. This is the same structure observed in other studies (McHugh 1958, Fuller 1960, and Engelhard 1970). The number of animals observed in these groups ranged from 3 (two cows and one calf observed in April 1969) to 240 (group size observed during the rut in August of 1968). Frequencies of occurrence of group sizes are presented in Fig. 12. There was a greater frequency of groups numbering more than 30 when compared to sizes observed in forested habitats by Fuller (1960:13). The distribution of mean group size for the study period is more erratic than that shown for bull groups but does

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indicate a decrease in size of cow-calf groups during the pre-calving season in April and in October following the roundup when the animals were more dispersed (Fig. 13). The large increase in mean group size in July of 1968 as compared to the 1969 figures is attributed to sampling bias as the author was in the process of becoming familiar with the area during June and July of 1968.

Cow-calf groups frequented areas in the northern and eastern parts of the park more than lone bulls and bull groups. Figure 14 shows the distribution of cow-calf groups during the non-breeding and non-calving seasons for the study period. Fifteen of the observations in the southwestern portion of the park resulted from movements of cow-calf groups to this area when helicopters were flying over the northern portion during attempted elk roundups in January 1970. The groups continued to frequent the northern and eastern portions of the park during the calving seasons (Fig. 15). Ten of the observations in the extreme southwestern portion of the park during that period were the result of one large group moving directly to that area after the author and two other riders on horseback surprised them in the Sanctuary prairie dog town (Fig. 6). The groups remained in the upper portions of the park during the rut of 1968 and 1969 but were seen in the southwest region following handling in the roundups of both years (Fig. 16). The corrals which the animals were handled in and released from are in the northern part of the park (Fig. 2).

"Solidarity" of activity was much more common in cow-calf groups than in bull groups. In all instances but one, group activity was initiated by a cow, usually with a calf. The one exception occurred when a calf was

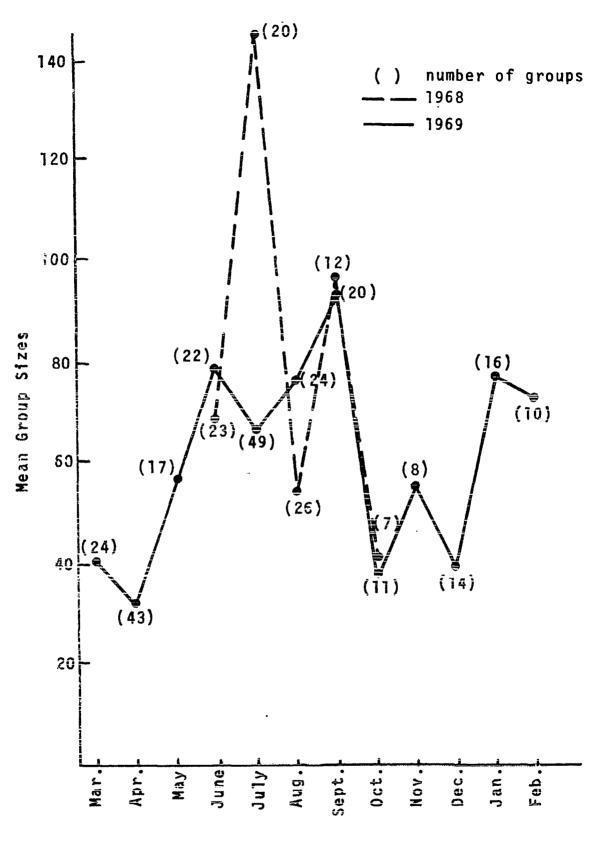


Fig. 13. Mean distribution of cow-calf group sizes at Wind Cave National Park

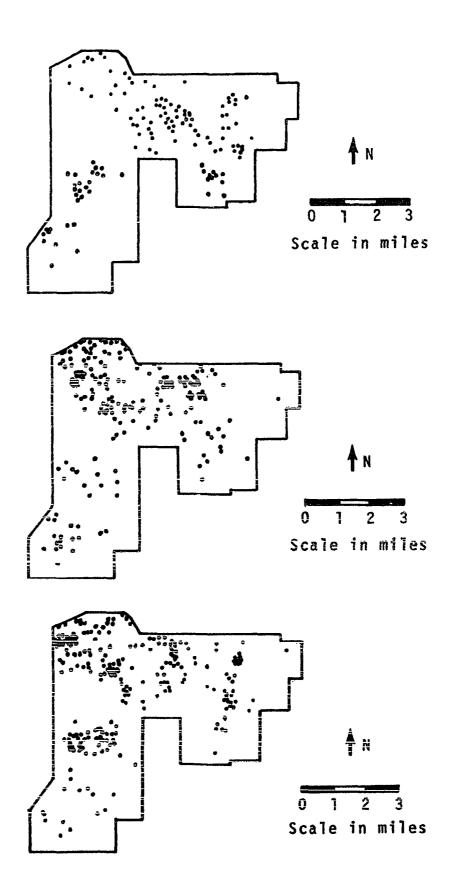
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Fig. 14. Distribution of cow-calf groups during October 1968, March 1969, and October 1969 through February 1970. This represents the fall and winter distributions and excludes the calving and breeding seasons at Wind Cave National Park

Fig. 15. Distribution of cow-calf groups during June 1968 and April-June 1969. This represents the calving seasons at Wind Cave National Park

Fig. 16. Distribution of cow-calf groups during July-September of 1968 and 1969. This represents the breeding seasons at Wind Cave National Park



struck and killed by a car at night in May of 1969. While I was field dressing the calf, the cow-calf group milled around in an excited manner approaching as close as 10 feet. Although this was not during the rut, one 5-year old bull was with the group. When the group dispersed from the area following the removal of the carcass, a portion of the animals moved off following the bull. This case, however, was not typical of the usual pattern.

Grazing patterns will be discussed with ingestive behavior. However, it may be pointed out that grazing in cow-calf groups generally was initiated by a cow standing and beginning to graze in place. When other members of the group began grazing, the cow that started the grazing or another might move off grazing and the group would follow. The cow tagged with radio channel 7 provides an example of how a cow with a calf influenced leadership. As already mentioned, this cow was tagged during the 1968 roundup. The reason for tagging this particular animal was that she continually broke away from groups being driven into the pens causing others to also escape capture. It was thought that this might indicate that this cow was a group leader. However, the cow was never observed in a lead position while grazing with cow-calf groups until July 18, 1969 following the birth of her calf. After that date until she lost the radio collar in the 1969 roundup she was frequently identified as the animal initiating activity and leading grazing groups.

McHugh (1958) also observed the frequency of leadership of cow groups by an adult cow. Fuller (1960:7) cites Soper (1941) and Siebert (1925) as attributing the positions of "herd leader" to a "majestic bull." Custer

(1962) and other writers also refer to the "patriarch" of a herd. In areas where mixed groups as defined by Fuller (1960:11) predominate this may be the case. However, with the one exception already noted, bulls were never observed in a leadership position of cow-calf groups at Wind Cave, even during the rutting season. Fuller (1960:7) points out two situations in which bulls were observed leading mixed groups. One of these entailed bulls taking the lead through deep snow. As no snow over 6 inches was recorded at Wind Cave during the study period and no accumulations of snow, this pattern was never observed. The second situation described by Fuller (1960:7) was when a mixed group took flight from the observer due to flight initiated by a "rear-guard" bull. Only one observation approximating this type of activity was noted at Wind Cave. On June 7, 1968 at 1900 hours MDT (approximately 30 minutes before sundown), I attempted to stalk a group of 90 bison with 35 calves. A group of 5 old bulls was observed lying 500 yards north of the main group. As the daylight was limiting, the approach was made from upwind. I was out of sight of the bison behind a ridge during the approach. As the top of the ridge was reached, a great deal of grunting could be heard from the cows. A look over the ridge revealed that the cow-calf group was moving off to the south at a trot away from the author. The five bulls were looking in the direction of my approach. As soon as I was seen by these bulls they turned and broke into a trot following the cow-calf group. As the groups were moving quite rapidly, it was impossible to follow them. However, at a distance of one-half mile they split, the cow-calf group going in one direction and the bull group in another.

Whether or not the bulls alerted the cow-calf group is not known, but they did not remain with the cow-calf group after taking flight. In any case, the only clue of my presence had to be scent as the bison could not have seen the approach from behind the ridge. Grinnell (1904) thought that bulls brought up the rear because they were slower to flee and not because they were protecting the herd. This is probably the case in the above description.

Observations during the roundup add support to the idea that cow-calf groups (even including bulls) rely on cows for leadership. When the animals were stampeded with helicopters, horses, and vehicles towards wing fence traps, the cows were observed in the lead. If the lead cow broke away before entering the trap, the rest of the group followed and the chase had to begin all over again. If, on the other hand, the lead cows entered the trap the rest of the animals usually followed. On occasions when the group split and part did not enter the trap, it was always a cow which initiated the movement. For this reason it was found that successful hazing of the animals depended not only on men and machines pursuing the animals from behind but also pursuit along the flanks of the groups to try to prevent breaking away by lead animals.

Flight distances for cow-calf groups showed seasonal variation. During the calving season (April through June), cow-calf groups were difficult to approach except by careful stalking. Approach to distances closer than one-quarter mile commonly caused the groups to take flight during this period. As an example, on April 29, 1969 (8 days after the first calves of the year were observed on the area), I was sitting by a

waterhole at the north end of Sanctuary prairie dog town in the study vehicle. A group of 30 cows and young bulls with 8 calves were observed emerging from the trees and walking in the direction of the vehicle. There were three cows with calves in the lead. At 400 yards from the vehicle, the lead cows turned and began running back towards the timber with the remainder of the group joining them. The group moved single file up a rocky slope (approximately 20% slope and 300 feet above the valley floor). The group slowed to a trot half way up the slope and then to a walk near the top where the slope was very acute. They moved over the ridge and out of sight. One 3-year old bull with the group did not follow but did move off into timber.

Engelhard (1970:22) also experienced this increased wariness by cows during the calving season. As in his study, this wariness decreased in June at Wind Cave and ceased with the beginning of the rut. McHugh (1958:15) reported flight distances for cow groups at 200 to 1,000 feet or more.

At the end of June and in early July with the beginning of the rut, I had little difficulty in approaching cow-calf groups. Although groups were excitable during the rut with the influx of bulls, the study vehicle could be driven into the middle of groups where trails permitted it. I believe that the bison became somewhat accustomed to this particular vehicle during the course of the study, possibly recognizing it by its unusual shape. Loud activity inside the vehicle would disturb the animals but quiet observation and speaking into the tape recorder in a low voice did not cause the animals to take flight. Initial entry into

these groups caused increased vocalization among cows and calves and also among bulls as the rut progressed. However, when the vehicle was stopped and the motor shut off, the vocalizations subsided (except for bull activities associated with courtship). The vehicle did not frighten the animals as they frequently approached to rub against it. On one occasion a calf approached and licked my hand which was extended outside the vehicle. Herrig and Haugen (1970:261) reported a similar incident at Ft. Niobrara National Wildlife Refuge in Nebraska.

Cow-calf groups were also wary of human approach for a short period following the roundup activities. Groups of bison which had been harassed would inevitably flee from the approach of the study vehicle or a man on foot or horseback. This fear subsided quickly, however, and the groups returned to normal within three weeks after handling.

Habitat preferences for cow-calf groups are based on 1123 observations (Appendix Table 4). Of that number, 823 (74.3%) were in grassland, 196 (17.5%) in prairie dog towns, and 104 (8.2%) in woodlands. Again a seasonal preference was observed for prairie dog towns during the summer months. In 1968, observations for June-October showed that 85 (92.4%) of the observations in prairie dog towns occurred in June-August. On a 12 month basis in 1969-70, 62 (59.7%) of 104 observations in prairie dog towns were recorded for May-August.

Koford (1958:69) cites King (1955) as reporting groups of 150 to 300 bison remaining on the Shirttail Canyon dog town (Fig. 2) at Wind Cave for as long as a week with drastic effect on the vegetation. In 1968 and 1969, the longest period of bison remaining on a dog town without

leaving it was two days in July of 1968. Leaving the dog town was defined as any movement away from it even if it involved only moving past the outside perimeter to graze on taller grasses a short distance away. The trend of increased use of dog towns during the summer months was definitely noted during the study. Larson (1940) points out the probability that bison grazing maintained the short-grass association before domestic livestock entered the Great Plains. Koford (1958:70) carries this further in saying that before the white man invaded the plains there was a reciprocal ecologic relation between bison and prairie dogs with each tending to maintain the short grass interspersed with patches of forbs and bare ground which was ideal habitat for the other. As prairie dog towns comprised only 3.2% of the area available to bison at Wind Cave, the relatively high percentages of observations during the summer months tends to support Koford's statement.

#### Vocalization

I have found no analytical work which provides definitive descriptions of the sounds made by bison. Such work would necessarily entail tape recordings of bison sounds which could be subjected to sound spectograph analysis. McHugh (1958) and Fuller (1960) present the best summaries of bison vocalization. Sounds are, however, difficult to describe and may depend on the ear of the observer.

The main vocalization heard during the study coming from cows and calves was the grunt. The grunting sound of cows is not unlike that of the domestic pig, although it varies in intensity and frequency. Cows

calling to calves when they become separated or when the group is disturbed (as in the initial approach of an observer) issue a series of grunts at a frequency of one per second. Calves answer with grunts which can be distinguished from the grunts of the cows by the higher pitch. Cows also grunted when moving but at a much more irregular frequency and lower volume than when calling calves.

McHugh (1958:6) described a "threat grunt" from a cow on a hay feeding area as the animal advanced on nearby bison or when other bison or humans approached her calf. The only sounds that might approximate these threat grunts at Wind Cave were from cows confined in corrals during the roundup. These grunts were louder and only issued one at a time. A very similar grunt was sounded by an animal when struck by another, especially from calves and juveniles.

Buils older than 5 years were never heard to make a grunting sound like the ones from cows. A sound described as a snort by McHugh (1958:26) was heard at Wind Cave. This is a puffing sound made by quick contractions of the abdominal muscles to force blasts of air through the nostrils. The snort was most commonly given by adult bulls entering or moving through cow-calf groups. The frequency varied from one to three seconds for this sound. It was usually accompanied by a wagging back and forth of the head as the bull walked along. McHugh (1958:26) stated that this sound carried at least 4,000 feet in still air but was difficult to hear under windy conditions. The distance was not that great for hearing this sound in the Wind Cave study, but this may be a function of auditory acuity of the author.

The most commonly heard sound made by bison bulls is referred to by several authors as the bellow (McHugh 1958, Fuller 1960, Fisher 1968, and others). This \_\_ound might better be described as a roar to separate it from bellowing in domestic cattle which it only remotely resembles. The roar is associated with high levels of excitement. When bulls are heard roaring almost continuously, the observer knows that the rut is in progress. The sound is something akin to the roaring of an African lion. It is produced by strong contractions of the abdominal muscles with the mouth open. Frequently the tongue protrudes when the roar is of high intensity (Fig. 17).

Roars varied in length from 1 to 6 seconds. The duration appeared to depend on the state of excitement in the animals. Loud, long roars commonly preceded a confrontation between two large bulls. A bull courting a cow would roar occasionally but would increase the frequency, volume, and duration of its roars if challenged by another bull. Roaring could be stimulated during the rut by the approach of a vehicle. It was also a common reaction to the excitement which resulted when a member of a group was shot or struck by a vehicle. Bulls will mill around, roar, and engage in various threat displays when a member of a group is killed, especially if the animal is field dressed. It is quite possible that the smell of blood triggers the excitement.

Roaring may well be one form of "displacement activity" (Tinbergen 1952:24-26) exhibited by bison bulls. Animals in conflict situations sometimes show behavior which appears irrelevant to any of the tendencies which are in conflict (Hinde 1966:278). Roaring does not fall perfectly

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Fig. 17. Adult bull bison (radio channel 1) roaring during the rut in 1968 at Wind Cave National Park. In this activity the tongue usually protrudes from the mouth as shown



into this category as it is a part of courtship activity as well as aggression. Strictly speaking, a displacement activity is one not related to courtship or aggression which appears when these conditions seem imminent. However, roaring does serve as an alternative to combat in the bison. Could it be a means for confusing or distracting an opponent to avoid combat? Other more recognizable forms of displacement activity will be discussed later.

### Grooming Behavior

Hafez and Schein (1962:289) discuss licking and tail switching as the two principal grooming activities in domestic cattle. While both of these activities are practiced by bison, the most obvious grooming activity is that of wallowing (Hornaday 1889, Garretson 1938, Goodwin 1939, Soper 1941, Roe 1951, McHugh 1958, Fuller 1960, Fisher 1968, Herrig and Haugen 1970, and others).

Wallowing consists of an animal dropping to its knees and then lowering itself with its hind legs to a position of sternal recumbency. The animal then rolls over onto one side and reaches forward with its legs. This is immediately followed by a kicking backward with all four legs with dust being thrown over the body by the action of the two legs in contact with the ground (Fig. 18). There is great variation in this activity. Sometimes the animal will sniff, horn, or paw the ground prior to actually wallowing. Also the wallowing may be preceded by rubbing the chin on the ground (Fig. 19). Following wallowing activity, bison, particularly bulls, may return to sternal recumbency on their knees and

rub forward and backward, extending the neck to give impetus to the thrust (Fig. 20). This movement appears to be a scratching of the abdomen and butt region. Great variation also exists in the numbers of times an animal will wallow, depending on the degree of excitement. Bison were never observed to roll completely over while wallowing except in one instance. That observation was made on a calf which rolled completely over once in the manner in which a horse does at times. McHugh (1958:5), Fisher (1968:90) and Herrig and Haugen (1970:251) all report never having observed a bison roll completely over. These authors attribute this to the hump making such an action impossible. However, with the exception just mentioned, calves were never observed to roll completely over despite the absence of the hump during the first three months of their lives. Bison calves began wallowing during their second week.

Adult bull bison wallow more frequently than do cows, calves, and juveniles. As evidence of this, these bulls lose the shed winter hair as early as June while cows may retain this hair in large patches throughout the summer and early fall (Figs. 21 and 22). This increased frequency of wallowing in bulls is at least partly due to the approach of the rut when wallowing is used as a displacement activity during agonistic encounters. Wallowing at such times does not show the grooming characters of scratching and rubbing, but rather entails vigorous horning and pawing of the ground followed by equally vigorous wallowing. During these periods of high excitement the bulls usually urinate while wallowing. Wallowing during the rut may reach such intensity when practiced by several courting bulls that the entire group is enveloped in a cloud of

Fig. 18. Bull bison wallowing. The two legs next to the ground are used to throw dust over the animal. Adult bison never roll completely over during this activity

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Fig. 19. Bison cow rubbing chin on the ground. This activity frequently precedes or follows wallowing. The head is moved back and forth to the animal's left and right

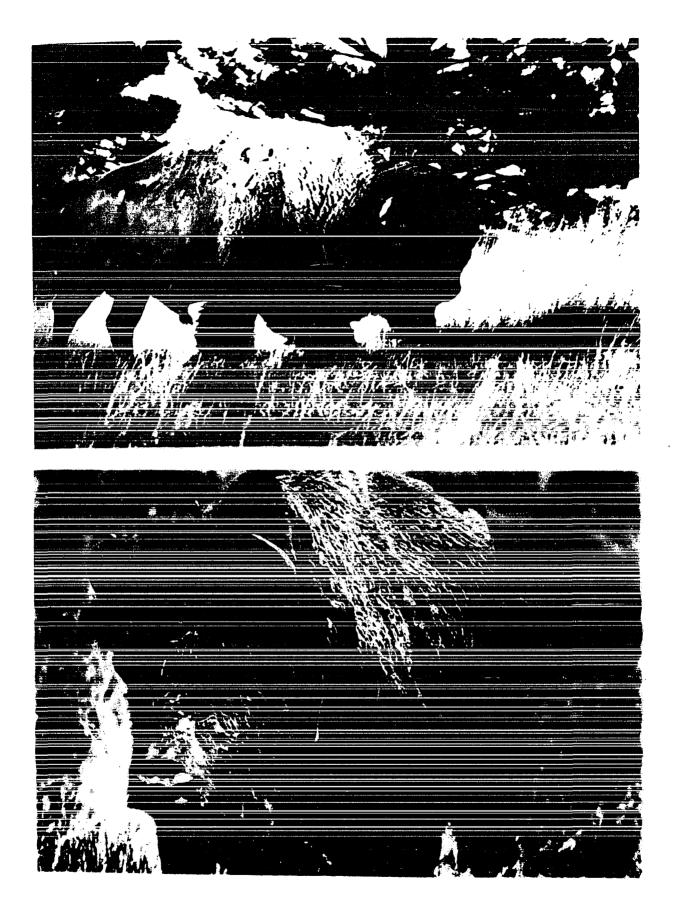
Fig. 20. Bull bison rubbing on the ground. In this activity the animal rubs forward and backward with the neck extended. This movement appears to be a scratching of the abdomen and butt region



Fig. 21. Bison bull with most of the shed and loose hanging winter hair gone. This picture was taken in early June 1968. This clean shedding is due to the greater frequency of wallowing by bulls than by cows. Bison shed winter hair from the back one-half of the body. The long hair on the shoulders, head, and forelegs remains throughout the year

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Fig. 22. Bison cow with relatively little loss of winter hair. This picture was taken at the same time as Fig. 21. Although the cow may not completely lose the winter hair until August or September, the shedding pattern on the body is the same as in bulls, from the rear forward



dust (Fig. 23). This nervous wallowing is also evident when bulls are disturbed, as by the approach of a human or vehicle. Such approach to bulls which are lying down frequently stimulates the wallowing activity followed by the bull standing up and staring at the intruder.

Bison prefer areas denuded of vegetation as wallowing sites. This helps explain the more intense use of prairie dog towns during the summer months when wallowing is at its peak. The dog burrows provide excellent dusting sites for the bison along with other bare areas found in dog towns. King (1955) also observed that burrow mounds were favorite wallowing sites for bison and that bison paw and horn mounds to fragments before lying down and rolling.

In addition to prairie dog mounds, bison use traditional wallowing sites which they have created by horning and pawing the sod and which are maintained through continual use. These sites are historically termed wallows and are shallow bowl-like depressions varying in size with the amount of use. These wallows were observed over the entire park during the study period. Custer (1962:15) commented that these wallows were common throughout the Great Plains and acted as catch basins for rain water due to their compacted soil conditions and bowl shape. Although stagnant, the water in these wallows apparently was used by early plainsmen when other water was not available.

Rubbing on inanimate objects is another grooming activity observed in the bison. Trunks of trees on the area were used as rubbing sites by the bison with the result that the bark was often removed from frequently used trees (Fig. 24). Besides older trees, small, bushy pines were used

Fig. 23. Bull bison wallowing while in a cow-calf group during the rut. This wallowing is part of the agonistic behavior associated with courtship activity and reaches such intensities that the entire group is enveloped in a cloud of dust

Fig. 24. Rub tree. Bison frequently use trees as rubbing sites. Trees frequently used for this purpose are usually denuded of bark. Occasionally horn scars can be seen on these trees where the bison have hooked at the tree during grooming



for rubbing, particularly for rubbing the head and chin areas. This was accomplished by thrashing back and forth with the head on the young pines which left these trees broken and deformed. Rocks were used as rubbing sites by the bison. One particular rock (Fig. 25) apparently had been used for some time as an 8-inch deep depression was found trampled into the ground around the rock where bison were observed scratching on it.

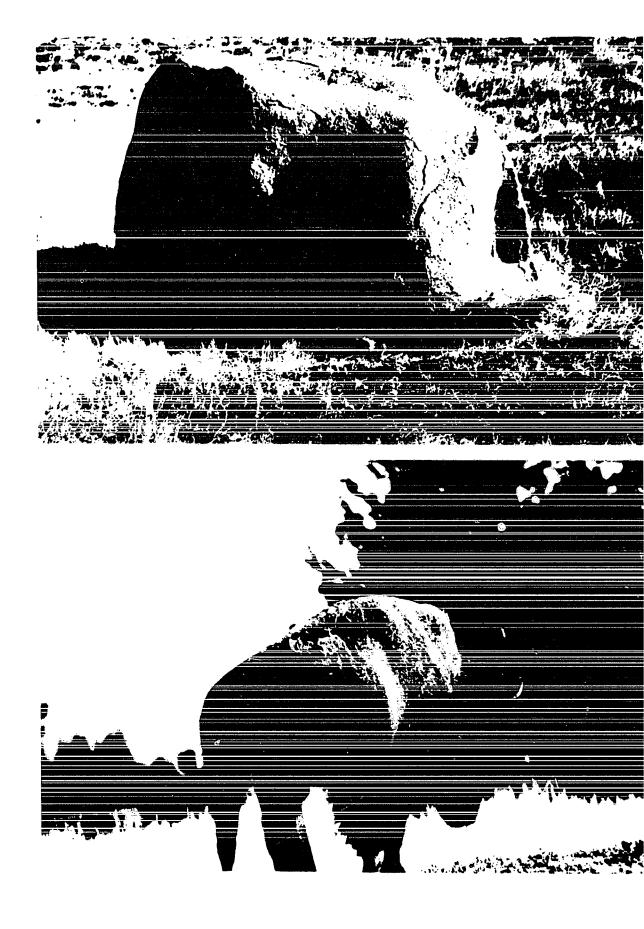
Man has made a contribution to bison rub sites through signs and roadside posts. Posts 17 inches high placed along the roads were frequently used as rubbing posts by adult bulls (Fig. 26). The height of the posts made them ideal for scratching the abdomen and external genitalia. This information should be of interest to visitors to the area as on at least two occasions people observing this activity reported to park personnel that an old bull bison was "hung up" on a roadside post and should be assisted in freeing itself.

Bison have what is sometimes an amazing capacity to reach various parts of their bodies during grooming activities. The animals increase in size from 30-70 pounds at birth to weights of around 1000 pounds for adult cows and more than 2000 pounds in adult bulls (Bureau of Sport Fisheries and Wildlife 1965:3). Yet, they are capable of licking all parts of their bodies with the exception of the under part of the chin and neck, the chest region, the head from above the nose back, the center of the back, and the perianal region. The remainder of the body is often licked during grooming activity. Rear hooves are brought forward to scratch the head and neck region and around the eyes with surprising dantiness (Fig. 27). Horns are used in cows and young bulls (before the tips are broken

Fig. 25. Bison rub rock. This particular rock apparently had been used for some time as an 8-inch depression seen around the rock was trampled into the ground by bison using it as a rubbing site.

Fig. 26. Bull bison using roadside post as a rubbing site. These 17 inch high posts were convenient locations for adult bulls to rub the abdomen and external genitalia. Visitors observing this activity sometimes thought that these bulls were caught on these posts and should be assisted in freeing themselves

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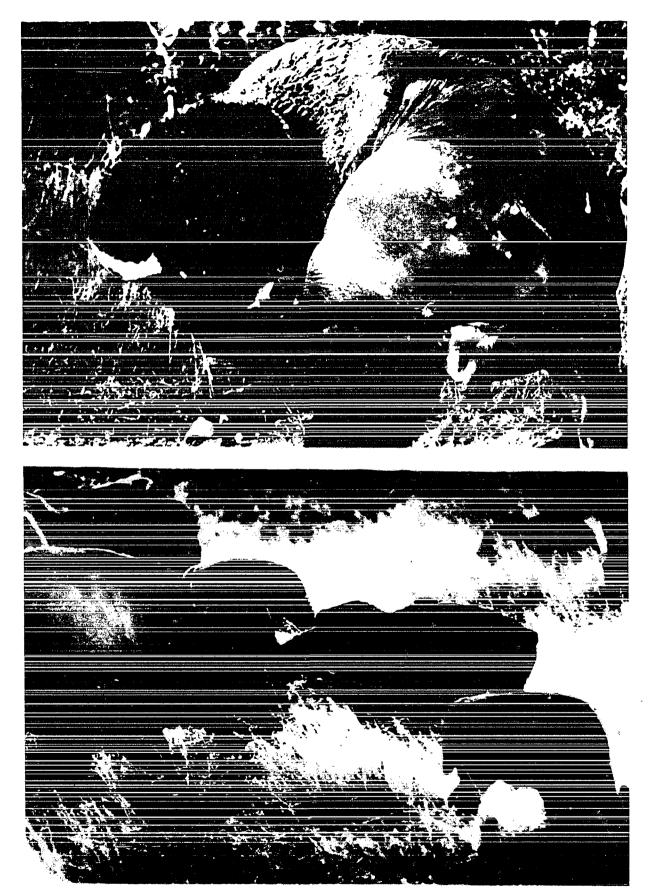
and worn) to scratch the hump region. Calves frequently use the front hooves to rub over the ears in the manner of a dog.

Mutual grooming was common among juvenile bison and particularly between cows and their calves. Fuller (1960:6) observed one instance of mutual grooming of two adult males but this activity was never observed at Wind Cave. Observations of mutual grooming at Wind Cave were limited to licking behavior. Brownlee (1950) described licking of individuals by herd-mates in domestic cattle. In his study, 95% of the licking interactions involved only the head, neck, and shoulder of the animal being licked. As a general observation, this pattern probably holds true for bison with the exception of grooming of a calf by a cow. During the first two weeks of a calf's life the cow frequently licks it over the entire body including the perianal region and the umbilicus. Calves, in turn, lick cows, but again mainly around the face and head. Calves will, however, rub their chins over the top of cows which are lying down (Fig. 28).

Tail switching is a part of grooming behavior in that it is commonly used to brush flies and other irritants from the surface of the skin (Hafez and Schein 1962:289). While the tail of a bison is only about one foot in length and not nearly as long as that of a domestic cow, it is used in a similar manner with increased activity during the summer months. This was especially obvious when the author visited a herd of bison at Land Between the Lakes, a Tennessee Valley Authority recreation area located on the Kentucky-Tennessee border. Insects appeared to be more of a problem for the bison in that herd and the animals responded with

Fig. 27. Adult bull bison grooming. This bull used the rear hoof to scratch the region around the eye. As shown in the picture, he then licked the rear leg from the hoof upward

Fig. 28. Bison calf rubbing its chin on a cow. Calves frequently rub in this manner on cows which are lying down. Usually the calves only lick the cows' head and neck region



vigorous and continuous tail switching. Tail switching was also noted in young bison calves at Wind Cave when they were suckling, although this activity is probably not a grooming response. Hafez and Schein (1962:289) recorded this same activity in calves of domestic cattle.

## Ingestive Behavior

Ingestive behavior refers to the sequence of events leading to and culminating in the intake of food or water (Hafez and Schein (1962:247). Since the same organs are involved in eating and drinking, it is convenient to use the broad term "ingestive behavior" to include both (Scott 1958: 17). Although suckling by calves is a form of ingestive behavior, it will be discussed later as a part of cow-calf relationships.

# Grazing behavior

Grazing behavior patterns in this study are based on 1055 observations (Appendix Table 2). As bison are large grazing ruminants, a great deal of time is spent on this activity. Bison, like cattle. differ from other grazers such as horses in the way they take in grass (Hafez and Schein 1962:248). Horses have both upper and lower incisors and grasp grass between their teeth to tear off a mouthful. Cattle and bison lack upper incisors and must use their tongues as prehensile organs. A horse pulls its nose back when cutting grass while a bison moves its nose forward. When bison take a bite, the tongue emerges from the mouth, encircles a small stand of grass, and draws it into the mouth. A pinching action between the tongue and lower teeth then binds the grass so that it can be torn off. This activity takes place approximately 3 times

in every 2 seconds in actively grazing bison. Mouthfuls are swallowed with very little chewing. Complete chewing occurs in rumination during the next loafing period. Hafez and Schein (1962:248) cite Voisin (1959) as stating that the structure of the lower jaw in cattle makes it impossible to graze closer than one-half inch from the soil while sheep can graze virtually at soil level. This same comparison holds true for bison.

Bison groups generally grazed actively during five periods of the day--just at dawn, just before midday, in the middle of the afternoon, one or two hours before sunset, and frequently around midnight. Wardrop (1953) observed a similar patterning in grazing behavior of dairy cattle in England. This pattern was not a rigid one with the bison, however, and varied with the type of group and local conditions. As example, during the rut, courtship activity disrupted the pattern and grazing periods were more random. Also, a combination of low temperatures and high wind often caused groups to remain inactive except at dawn and dusk when the winds usually diminished. Herrig and Haugen (1970:246-7) observed a pattern very similar during the summer months at Ft. Niobrara. Egerton (1962:9) recorded three grazing periods between 7:00 a.m. and 10:00 p.m. in the captive Waterton herd and cited a similar pattern in domestic cattle from a study in New Zealand by Corbett (1953). She did, however, observe the same change in pattern in a high wind (Egerton (1962:14).

Grazing periods for bull groups and lone bulls followed the general trend but appeared to be more variable. For example, in a group of

5 bulls, 2 might be observed grazing while the other 3 were lying down. This made analysis of this type of activity for bulls more difficult. Fisher (1968:88) worked intensively with lone bulls in North Dakota and recorded feeding during all daylight hours with greatest activity between 6 and 9 a.m. and 3 and 6 p.m. At Wind Cave, bulls were observed grazing during all night periods as well. In all probability, it is the higher degree of allelomimetic tendencies in cow-calf groups which causes the grazing patterns to be more predictable.

Typically, grazing in a cow-calf group is initiated when a few members of a loafing group stand up and begin to graze in place. During loafing periods, group members are usually oriented randomly with respect to body axes. Within 15 to 30 minutes after the first members are up, the whole group (with the possible exceptions of a few calves) are up and grazing in place, but orientation remains random. If an older cow begins to move off grazing, the other members will follow and the group becomes oriented in the same direction. Such grazing activity progresses forward in a "wave" fashion, with members spread out laterally behind the leader(s). Figure 29 illustrates a group grazing in such a wave. Grazing movements vary from one-quarter mile to 3 miles. Time of concentrated grazing varies from 1 to 3 hours. As the leader(s) slows, the group begins to graze in place and gradually loses its directional orientation. Within 15 to 30 minutes after stopping, members of the group, one after another, begin to lie down and soon the group is again at rest in a loafing period. During the movement, cows with young calves occasionally stop feeding and utter a series of grunts urging calves which may have

been lagging behind to catch up.

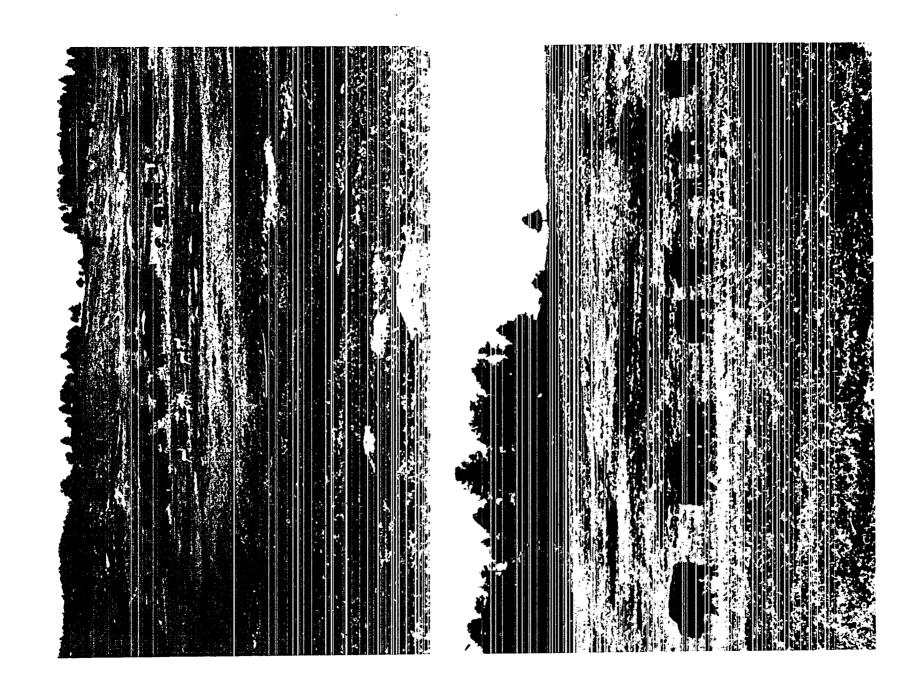
Bison groups randomly move from one location to another, often for no apparent reason. These movements do not involve grazing and can be distinguished from a distance in that the animals move in a column form, single file (Fig. 30). The longest such movement recorded during the study was 7 miles. This incident occurred in June of 1968. At that time there was no obvious stimulus to cause such a movement.

Rumination is another aspect of ingestive behavior. It involves regurgitating, remasticating, and reswallowing previously swallowed food (Hafez and Schein 1962:258). During grazing activity, large quantities of herbage are taken into and stored in the rumen after only cursory mastication. In the rumen, fermentation of the herbage is started. During loafing periods, boluses of food are regurgitated from the rumen and chewed more thoroughly. This type of ingestion permits the animal to take in large quantities of food in a short period of time and to further facilitate digestion of that food in a less vulnerable environment.

Bison ruminate during loafing periods which alternate with periods of active grazing. Herrig and Haugen (1970:249) reported lone bulls chewing each bolus 55 to 57 times. Fisher (1968:89) stated that his data on several ruminating bison indicated that each bolus was chewed 38 to 70 times at a rate of about one chew per second. I did not make exhaustive counts on chews per bolus. However, based on the observations made and previous studies, it seems that the number of chews per bolus is quite variable and may reflect individual variation, differing size of the boluses, and varying quality of the ingesta. Hafez and Schein (1962:259)

Fig. 29. Bison grazing in a "wave" pattern. Bison typically move in this fashion while grazing. The group spreads out laterally behind the leader(s) and may move from one-quarter mile to 3 miles

Fig. 30. Bison moving in column fashion. This type of movement occurs when bison are moving from one area to another but not grazing as they go. It is frequently associated with movements to water or salt. This single file type of movement is probably the activity which gives rise to the bison trails



cite evidence that ruminating time varies with the quality of forage.

### Drinking behavior

Water was available for bison from 4 ponds, 6 concrete spring fed watering tanks, and 2 streams (Fig. 2). In the summer of 1969, two of the ponds were dry most of August. Standing water was available following rains. Although this standing water was usually stagnant, the bison made use of it as a water supply.

During the summers of 1968 and 1969, cow-calf groups visited watering areas at least once a day. When temporary potholes began to dry up in early August, these groups made use of more permanent ones, particularly one located at the north of the Sanctuary prairie dog town. Bull groups were observed using watering areas during the summer months but not with the frequency of the cow-calf groups. This conclusion may be biased, however, as the bulls could have been using standing water or watering tanks in remote areas not regularly checked. Fisher (1968:89) observed that lone bulls did not go to water once a day. McHugh (1958:5) stated that bison went to water at least once a day in all herds he observed. He further observed that the most heavily grazed areas on the National Bison Range were near water holes.

As mentioned previously, a time lapse camera was set up on a watering area for 97 days from August through November of 1969. This was a stock pond located one-half mile from the Sanctuary prairie dog town. The camera exposed one frame of film every 5 minutes during daylight hours and covered the entire pond. Bison were observed using the pond on 19 of the 97 days. This included 10 morning and 5 evening visits by cow-calf groups

and 6 morning and 4 evening visits by lone bulls. As individual recognition was not possible, the exact numbers of animals involved is not known. Ten of these visits were made August through October. The remaining 15 visits were made from October 28 to November 16. During these same periods bison were observed watering at other locations on 55 separate occasions. On only one occasion did the bison spend extended time at the pond covered by the camera. In August, one cow-calf group spent an entire morning around the pond being monitored.

During periods when bison remained in the vicinity of a pond the animals moved to and from the water in a single file. When bison moved to a watering area from another location they also followed this single file pattern. The lead animals, as usual, were cows with calves. When the bison were within 100 yards of a watering area, the animals usually broke into a run and then slowed to a walk at the water's edge. Bison characteristically wade out into the water before drinking, even the calves (Fig. 31).

One interesting behavior pattern not previously observed is that both bulls and cows almost invariably urinate into the water upon wading into it. This micturition response only occurred when bison actually waded into the water. Herrig and Haugen (1970:250) observed that both urination and defecation occurred often near watering tanks. Bulls were observed to walk 60 to 100 feet away from tanks before urinating. The watering tanks at Ft. Niobrara where these observations were made are not constructed such that animals can wade into them as are the concrete tanks at Wind Cave.

McHugh (1958:5) observed that bison ate snow in the winter when water holes froze over. Bison were also observed eating snow at Wind Cave, although, as mentioned, previously, heavy snows did not occur during the study. Close observation is necessary to determine the difference between bison eating snow and sweeping it away for grazing purposes. Bison characteristically use the nose and chin to clear snow from forage rather than pawing as horses do.

When ice covered small puddles, bison at times broke through with their noses or front hooves. Holes made in this manner by bison were also observed being used by pronghorns (<u>Antilocapra americana</u>) and infrequently elk.

## Salt block use

Salt blocks were placed at six locations on the area by park personnel. The blocks were placed at locations where they could not be seen from the roads by visitors but where they would attract animals to areas where they could be seen by the visitors (Fig. 2). Bison visited these salt areas but not on a regular basis. The bison consumed the salt by licking the blocks, whereas horses on the park frequently chewed on the blocks placed in their corral. As the blocks were not placed in boxes, they were readily dissolved by rain. This resulted in the bison licking and eating the soil in the vicinity of the blocks. McHugh (1958:6) observed that bison ate the mud from natural licks. One spot in the Research Reserve prairie dog town at one time some years earlier had been used as a salting area. Despite the lack of recent salting, bison frequently licked and chewed the soil at the spot when they were in the

Fig. 31. Bison watering. The animals typically wade out into the water to drink. Both bulls and cows frequently urinate into the water. Calves also wade in to drink as shown in the picture

Fig. 32. Bison calf defecating. This posture is typical of the adult bison as well as calves. The hind legs are brought slightly forward and the back is humped somewhat. The tail posture is also typical of this activity



area.

#### Eliminative Behavior

Eliminative behavior in bison includes the postures and circumstances associated with urination and defecation. These activities are not only mechanisms for voiding the body of waste materials but are also indicative of certain behavior patterns in which the evacuation of wastes may be more an indication of mild excitement than the prime stimulus.

#### Defecation

Bison deposit their excreta haphazardly with respect to location. Such deposits or "chips" were observed in abundance in all areas frequented by the bison.

Typically, a special stance is assumed for defecation. The base of the tail is raised and arched away from the body. The hind legs are placed slightly forward and apart, and the back is arched. Figure 32 illustrates this stance by a calf. Bison generally defecate while standing in one place. Occasionally animals were observed to defecate while walking but never while lying down. The defecation stance tends to minimize soiling of the hind legs by feces. However, walking while defecating may result in the animal soiling itself.

Defecation rates were not recorded for bison during the study. Hafez and Schein (1962:285) report that frequency of elimination (both defecation and urination) varies widely with quality of feed, ambient temperature, relative humidity, milk yield in cows, and individuality of the animal. Herrig and Haugen (1970:250) report that defecation by lone bull bison is frequent. Their observations include 3 defecations in 3.7 hours, 5 defecations in 5.8 hours, and 2 defecations in 2.6 hours. These observations were made during the summer months. Rorabacher (1970:86) reports that temporary diarrhea in bison results from the change from dry forage to new grass in the spring. During these periods at Wind Cave the feces of the bison were more fluid and of a green color as compared to dark brown during the remainder of the year. This same phenomenon was observed in bison at Land Between the Lakes where the pasture was lush and succulent.

Defecation is an indicator of increased excitement in bison. This was particularly evident when the author approached bison in the study vehicle. Lone bulls typically would arise from a recumbent position or stop grazing when approached and then defecate and often urinate. This response was also noted in cow-calf groups. One might speculate that the posture associated with defecation had something to do with this. Hafez and Schein (1962:285) indicate that physical barriers which prevent domestic cattle from assuming a proper stance tend to inhibit, at least temporarily, the relaxation of the anal sphincter muscles. Thus, an electrically-charged wire which presents tail raising may, in turn, inhibit the passage of feces. In bison the raising of the tail is a feature of excitability in agonistic behavior (to be discussed later). It does not seem unreasonable to speculate that the raising of the tail with increased excitement caused by intrusion of a vehicle or another animal may act as a stimulus for relaxation of the anal sphincters resulting in defecation. This behavior pattern is probably the source of the axiom

that when a bull bison elevates his tail he may "charge or discharge."

### Urination

Female bison do not urinate while walking or lying down. Typically, cows assume a position much like that of defecation with perhaps a greater arching of the back. The urine is voided with some degree of force resulting in an arc of fluid extending 2 to 3 feet behind the animal. Hafez and Schein (1962:285) noted this same pattern in domestic cows and stated that this made contamination of the skin even less likely than during defecation.

Bull bison urinate with the tail elevated as in defecation but generally do not arch the back. Herrig and Haugen (1970:251) also reported this typical urinating posture in bulls. Also, bulls often urinate while walking with the urine dribbling from the sheath. Urine is passed slowly by bulls and with not nearly as much pressure as in cows. Examination of films taken during the rut, however, indicate that bulls tending cows may urinate while having a partial erection of the penis. This results in a forced squirting of urine under these conditions. Wickler (1969:144) cites evidence of ungulates urinating against their own abdomens during the rutting season. This type of urine marking is distinct from normal micturition as the urine is sprayed briefly and sporadically as in ejaculation. In fact, the ejaculation mechanism may be involved. Whether this urine spray in the bison serves as a marking mechanism is not known, but such an assumption is not unreasonable due to the marked difference from normal micturition. This activity, however, should not be confused with "eurination" (emitting a jet of urine at a conspecific) as

in some lagomorphs and rodents (Wickler 1969:145). The spray in bison was never observed to be "aimed" at another animals. Also, as bison are not territorial in the usual sense of the word (i.e. defending fixed areas of land), this squirting of urine must be assumed to be a "self-marking" mechanism rather than establishment of territorial boundaries.

Bull bison frequently urinate while wallowing, particularly during the rut. Mixed with the dust of wallowing sites, this causes mud deposits to adhere to the animals. Fisher (1968:91) stated that such wallowing sites have an offensive odor that could be detected from a distance of 4 to 7 yards. Bison do have a distinctive odor which is difficult to describe, although, to me at least, it is not particularly offensive. Engelhard (1970:9) discusses odor of bison in some detail. In his study he noted that bulls had a stronger odor than cows or calves but that this was noted throughout the summer and not restricted to the rut. Bison odor can easily be detected in areas that the animals have vacated. Allen (1876) noted the distinctive odor of bison from large herds more than a mile away. This odor can be used to locate bison before sighting them. Talbot and Talbot (1963) used this technique to track wildebeest (Gorgon taurinus) in East Africa. While the odor of bison is distinctive, I do not believe that it is entirely due to continual contamination of the skin with urine.

Frequent urination by bulls during the rut may possibly be related to changes in hormone levels, particularly testosterone. Fraser (1968:71) states that sex drive (libido) in male animals is dependent on the production of testosterone. He goes on to state that the highest degrees

of sex drive occur in those species which have the shortest breeding periods per annum, viz. those which rut. Klopfer and Harlman (1967:117), in referring to experiments with dogs, state that "frequency of occurrence of the micturition motor pattern of male dogs was shown to be quantitatively dependent upon the amount of androgen injected." Although I have never seen reference to comparable work done with the bison, it is possible that there is a relationship between the testosterone production of the rut and the micturition response in this species also.

Spontaneous urination by bison upon entering water has already been discussed with ingestive behavior. These frequent deposits of urine in watering sites did not prevent the bison from drinking from them.

# Agonistic Behavior

The word "agonistic" comes from a Greek root which means "to struggle" (Scott 1958:18). This may include any sort of adaptation which is connected with a contest or conflict between two animals. This includes escape and submissive behavior as well as aggresive initiation of combat. Agonistic behavior is most obvious among bison bulls in the rut.

Schein and Fohrman (1955) categorized the sequential patterns of agonistic behavior in cattle as "approach, threat, and physical contact." Allen (1967:11) has summarized a characteristic sequential agonistic pattern in bison from McHugh's (1958) work. The categories from the most gentle to the most violent are "(1) the direct look; (2) the head and horn shaking; (3) snorting; (4) pawing, wallowing or rolling; (5) the advance, accompanied by lowered head, erect tail, and bellowing; (6) the horn lock,

where the opponents advance slowly, mesh horns and engage in pushing and hooking; (7) violent charges, with vicious, quick horn jabs or thrusts head-on or to the flank to disembowel the opponent." The behavior does not always proceed in the above sequence, and some steps may be omitted.

These categories of behavior held true during the Wind Cave study with the possible exception of the last one. Actual combat situations between bison bulls were observed three times in 1968 and seven times in 1969. Most of these encounters lasted less than 1 minute with the longest lasting 1 minute and 45 seconds. There was one atypical encounter included in these which lasted a total of 17 minutes between the same two bulls. However, the bulls were not continually fighting but broke off at intervals. These bulls were approximately 8 years old and similar in size.

Fuller (1960:8) discusses the controversy as to whether or not fighting bulls charge one another. He cites Goodwin (1935), Cahalane (1947) and McHugh (1958) as all mentioning charges. His observations agreed with Garretson (1938) and Hornaday (1922) who state that the animals advance slowly. Observations at Wind Cave showed elements of both types of behavior. Bulls observed engaging in vicious combat approached slowly to within about 4 feet of each other while roaring continuously. Suddenly they lunged at each other, striking head on and hooking with their horns. In such encounters the power thrust appeared to be delivered with the hind legs. A great deal of dust was kicked up and patches of hair were torn from the head and neck region and thrown into the air as a result of the hooking action. In every case except one, combat broke off when one of the antagonists turned and walked away. In

that one exception, a 6-year old bull pursued another animal of the same age for 50 yards.

Whenever fighting broke out between two bulls, a notable increase in group excitement occurred. Other bulls began roaring continuously and rushed to the location of the two combatants. This included bulls of all ages from 2-years old and older. These bulls all demonstrated signs of high excitement with raised tails, horning and pawing the ground, wallowing, and urination. On no occasion, however, was another incident of combat triggered between other animals.

One atypical incident occurred on August 6, 1968 which involved agonistic behavior. This incident was caused when a group of bison were crossing a highway on a foggy night at 0215 hours. A commercial bus struck one of the bulls in the group due to the poor visibility. The animal ran off across the road. Immediately three bulls began fighting. One of these bulls was believed to be the animal which had been struck. I watched the combat with a spotlight. Two of the bulls alternated fighting with the third, the one believed injured. None of the bulls showed any indication of wounds, although it was difficult to determine under the lighting conditions. The fighting continued for 5 minutes before all three bulls ran out of sight. The bus, estimated to have been traveling at 30-35 miles per hour, was dented extensively.

The above incident may be another reaction similar to ones exhibited in the presence of dead animals or blood. McHugh (1958:8-9) made reference to this type of behavior. Hornaday (1889:476) noted that bison cluster around fallen animals and sniff at the warm blood. Allen

(1876:212) reported that hunters had to drive bison away from carcasses to prevent them from playfully goring a downed member. It may well be that the above fighting was stimulated by blood on the animal believed struck by the bus.

Fuller (1960:9) reported combat in bulls which was stimulated by the noise of low-flying planes. This was not observed at Wind Cave except for one instance recorded on film from a roundup held prior to the study. The film, taken from a helicopter, showed two bulls coming together for a few seconds with their tails erect and engaging in lunging combat. The two bulls broke off almost immediately. One unverified account reported a bull hooking up at a hovering helicopter during a roundup. Herrig and Haugen (1970:261) reported no reaction to low flying aircraft or sonic booms at Ft. Niobrara.

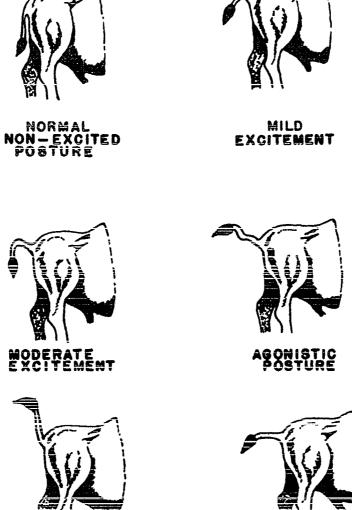
One category not included in Allen's summary (1967:11) was observed at Wind Cave. This entailed an animal jumping towards another with the front legs held stiff so that the animal bounced for a few steps. This behavior was particularly noted with animals in the corrals during the roundup. If an animal was left alone in a pen, it frequently became irritated by the noise and harassment. Movement along the side of the pen would cause the animal to jump forward in the stiff-legged wanner. Then the animal would paw or horn the ground before repeating the action. This was accompanied by a prolonged forced nasal wheeze which sounded like a 3-4 second hiss. Animals sometimes worked themselves into such a frenzy in this manner that they were quite difficult to drive out of the pen even after the gate was opened. This jumping threat was also observed

under normal conditions but without the accompanying hissing sound.

Agonistic behavior in cows included all of the categories mentioned except violent combat. Many encounters between cows and other bison resulted in the other animal moving away from the cow, but the action by the cow was often subtle and difficult to detect. Hooking at another animal was usually the most violent activity practiced by cows, although they would engage in pushing contests. This hooking was vicious when the animals were confined in corrals during handling. It was difficult to determine if those pushing contests which occurred under normal conditions were serious or forms of play activity.

Both cows and bulls can kick sharply and accurately with their hind hooves. Bison harassed with electric prods in the corrals often lashed out in the direction of the prod with one or the other of their hind legs. On more than one occasion, the 2 x 12 inch planks on the sides of the corral were cracked or broken by such blows. Under normal circumstances, cows were observed kicking at yearlings attempting to suckle. Two yearlings struck in this manner had the sheath knocked from one horn by the blow.

Except in the mildest forms, the raising of the tail is perhaps the best indicator of excitement in the bison (Fig. 33). In agonistic encounters, the degree of excitement may be gauged by the position of the tail. In mild encounters the tail is barely elevated. As excitement increases, the tail is elevated to higher levels. In actual combat situations the basel tail is held in a rigid manner perpendicular to the axis of the body. This condition was always noted just as bulls lunged





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Fig. 33. Tail postures in bison indicating levels of excitement

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at each other. However, when the bulls were locked in actual combat, the tail was brought down and held tightly against the perianal region. This may indicate that the tail serves as a form of visual communication in agonistic encounters but that the muscle strain involved in actual pushing causes the tail to be dropped. When bulls broke off between lunges, the tail was again elevated. The elevated position of the tail was easily recognized when bulls at Wind Cave faced bulls from Custer State Park with the boundary fence separating them (Fig. 34). Such encounters usually were restricted to pawing and horning of the ground and roaring, although the fence was occasionally bent by bulls hooking it.

To completely understand agonistic behavior, one must first know something about dominance and hierarchy. Scott (1958:203) points out that any group of animals that can fight can set up a dominance order. He further points out that dominance orders have a wide variety of functions, but all result in the division of something which is limited in supply, such as mates, territory, and food. Woodbury (1941:410) points out that it has been known for many years that a "hook order" or dominance hierarchy exists in domestic cattle.

Egerton (1962:18) states that accurate information on the social relations of herd members requires recognition of individuals. McHugh (1958) found a dominance hierarchy in a herd of 16 bison in Jackson Hole Wildlife Park in Wyoming. He distinguished the herd members as individuals by physical differences or painted markings. Egerton (1962:18) described the dominance hierarchy for a herd of 25 bison in Waterton Lakes National Park, Alberta. She identified individuals on the basis of sex, size, and

Fig. 34. Agonistic posture by a 3-year old bull bison during an encounter along the Wind Cave National Park-Custer State Park boundary fence. The degree of elevation of the tail along with pawing of the ground indicated the high level of excitement

Fig. 35. Pregnant bison cow (radio channel 7). The distended abdomen is the best criterion for identifying pregnant cows in the last two to three months of pregnancy. This picture was taken on March 13, 1969 but the cow did not give birth to her calf until the second week in July



individual characteristics such as shape of horns. It took five weeks for her to be able to recognize each animal individually.

Due to the size of the area and the numbers of bison involved, it was impossible to document the workings of a dominance hierarchy in the bison at Wind Cave. Although certain individuals could be recognized over the course of the study, the random observations of these individuals are meaningless as far as constructing continuous patterns of dominance. Also, the annual cull removed animals from the herd which probably upset any dominance scale which existed. As a general comment, however, many observations of encounters among members of the herd indicated that some mechanism was at work which precluded continuous combat. Schein and Fohrman (1955) found a strong positive correlation between the dominance status of domestic cattle with age and weight. They also pointed out that other factors such as individual agility and temperament were important in determining rank. On a purely subjective basis, both of these criteria appeared to be functional in bison during this study. Also, McHugh (1958: 17) reported that of 1,027 interactions observed in the Jackson Hole herd, 72.8% were passive dominances and 27.2 were aggressions. Although percentages of occurrence are not available in my study, it was obvious that passive dominances were at least this frequent at Wind Cave. In McHugh's study, more than 90% of the interactions were recorded during displacements on the feeding grounds. The animals he studied were fed hay during the period of observation due to the absence of natural food. This may have caused a somewhat higher incidence of aggressions than at Wind Cave where the animals feed only on grasses and are therefore more

dispersed. Kummer (<u>ca</u>.1970:11), in discussing space mechanisms in social behavior, points out that "by spacing out, an animal can remove itself from the compulsion to respond to its neighbors."

Mortalities attributed to agonistic encounters were recorded at Wind Cave during the study period. On August 24, 1968, a bull estimated at 10 years of age was destroyed due to a wound in the right hip. The wound was 4 inches in diameter and 4-5 inches deep. It appeared to have been caused by a horn. In addition to this wound, the hair along the back of the animal was sloughing off in large patches. The back and the wound were heavily infected with maggots. The wound had a putrid odor which could be detected 25 yards away. Survival was doubtful and the animal was destroyed for humane reasons.

In 1969, three cases of bull mortality were recorded following the rut. The bulls were all estimated as at least 10 years old. No external wounds were observed on any of these bulls. However, each had heavy infestations of maggots localized on the back of the neck and in the ears. Observations of hooking action of bulls in combat indicate that these regions are subjected to severe punishment during fights. A similar maggot infestation was observed on a live bull immobilized on August 22, 1968. This bull, age 10-12 years, was also blind in the left eye. Although conclusive evidence is lacking, it was assumed that these bulls found dead in 1969 died as the result of combat activity. None of the animals showed signs of emaciation which might have indicated possible disease. Also, due to the isolated locations of the carcasses and the lack of bullet wounds, shooting by poachers was not considered. One incident of calf mortality was observed during the study which may have been the result of agonistic activity. The carcass was discovered on August 11, 1969. The animal was a large, dark brown calf estimated at 3 months old. No external wounds were visible, although a portion of the carcass had been eaten by magpies (<u>Pica pica hudsonia</u>). A golden eagle (<u>Aquila chrysaetos</u>) was observed sitting in a tree over the calf and also had probably been feeding on carcass. The eyes had been eaten out and the anal region up into the abdominal cavity was partially eaten making sex determination impossible. There was no evidence that coyotes had been feeding on the carcass. The rumen was full of grass. Although predation was possible, the predators at Wind Cave were never observed to have taken bison during the study. As death occurred during the breeding season, it was believed that the animal was either killed in an agonistic encounter or trampled during a courtship chase.

McHugh (1958:28) states that several casualties of battle were recorded in his study. The majority of these casualties were older bulls. Fuller (1961:291-5) does not consider mortality from combat as a significant source of natural mortality. Bison were wounded by horn hooking, some seriously, during handling operations during the roundups at Wind Cave. However, due to the confined conditions and harassment in handling, these cases are not considered natural occurrences.

One other topic must be considered before leaving agonistic behavior. All forms of agonistic behavior with the exception of severe combat were observed among calves and juveniles. This type of activity, however, is probably best interpreted as play in which young animals imitate forms of

adult types of adaptation. Mounting behavior in these young animals also represents a playful form of sexual behavior. Scott (1958:28) observed this relationship in sheep and noted that, as the animals grew older, their behavior became more and more like that of the adults. It may well be that this type of behavior served as the basis for the development of a dominance hierarchy.

## Cow-Calf Relationships

Two studies are available which deal in detail with cow-calf relationships in bison and with the development of behavior of the calf. Egerton (1962) produced the first work with the bulk of her observations being made on a group of 25 animals. Engelhard (1970) worked primarily with two herds of approximately 133 and 183 animals at the National Bison Range in Montana. Besides these two studies, McHugh (1958:30-35) provides information on this type of behavior.

#### Calving rates and chronology

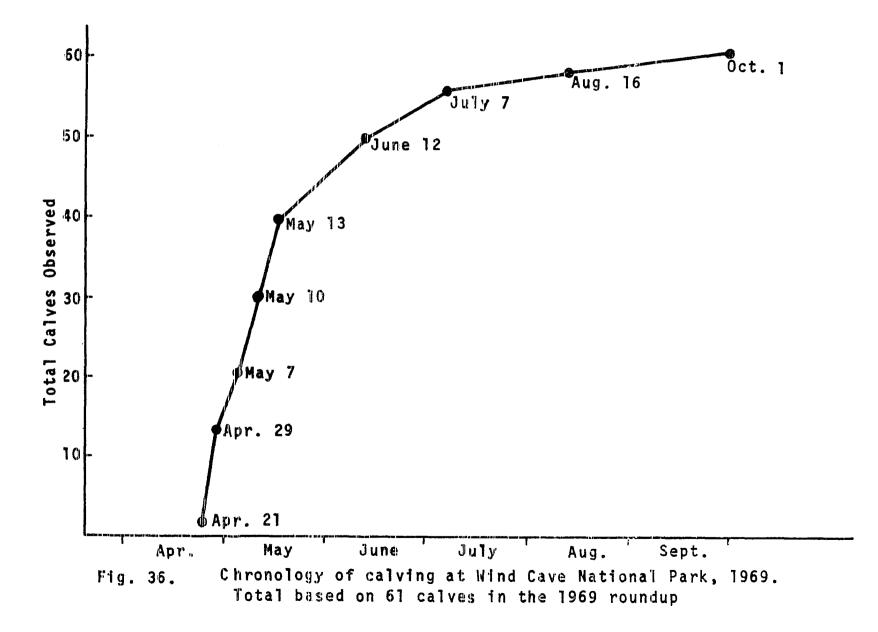
McHugh (1958:30) reports bison cows are sexually mature at 2 years and bear calves at 3 years. Fuller (1961:288) states that sexual maturity varies, and that a few precocious females breed as yearlings at about 15 months. McHugh (1958:31) also presents data which indicate that incidence of pregnancy declines gradually after an age of 12 years and markedly after 24 years. Burns (1953:128) reports that cows ear tagged 40 years prior to slaughtering were accompanied by calves at Wainwright Park, Alberta.

Using 2 years as the breeding age with no maximum, 78 cows were of calf-bearing age at Wind Cave in 1969. A total of 61 calves was handled

or observed during the roundup of that year. One case of calf mortality already discussed brought that number to 62. Assuming no loss of cows after the 1968 roundup and no other calf mortality, the calving rate for 1969 was 79.5%. As 63 calves were observed in 1968, the rate was approximately the same for that year, also. Calves were singles, with no evidence of twinning. Engelhard (1970:19) reported an initial production of 85% from 105 cows of calving age at the National Bison Range.

Sex identification was available for 124 of 125 calves produced in both years of the Wind Cave study. By chance, the combined ratio male: female was 50:50. Taking the two years separately, however, yielded unequal ratios. The 1968 male:female ratio was 57.1:42.9, while that for 1969 was 42.6:57.4. McHugh (1958:31) listed a ratio of 50.4:49.6 based on 1,465 calves sexed between 1941 and 1953 at the National Bison Range. He also showed unequal ratios of 57:43 in 1950, 55:45 in 1949, and 42:58 in 1942. Fuller (1961:287) reported a primary sex ratio (in utero) of 53:47 based on reproductive tracts from mature females.

Figure 36 shows the accumulative chronology for calving at Wind Cave in 1969. Figures for 1968 are not presented as the study period did not begin until well into the calving season and accuracy of total counts are probably not reliable while I was becoming familiar with the area. The values in Fig. 36 are based on total calves observed on the dates given. On these dates, field effort was devoted to surveying the entire area to get as accurate a count as possible of total calves. The first two calves were observed on the area on April 21. By May 13, a total of 40 calves was observed representing 64.5% of the years production. This time



period marked the peak of the calving season. Engelhard (1970:19) found the majority of calves born on the National Bison Range appeared during the second and third weeks in May. In Egerton's (1962:39) work with the Waterton herd, 11 calves were born in 1961--2 in May, 2 in June, 3 in July, 2 in August, 1 in September, and 1 in December. In 1962 she reported 4 calves in June, 1 in July, and 2 in August. McHugh (1958:30) reported the main calving season in the Lamar Valley of Yellowstone National Park was from April 15 to May 31 with a greater concentration of births in the central 2 weeks of that period. He also commented that the calving season was similar in the Wildlife Park and the Wind Cave herd. In all herds there is a scattering of calves born outside the main season.

Estimates of the duration of the gestation period in bison are 9 months (Brown, 1936), 270 to 300 days (Burns 1953:199) and 9-1/2 months (Seton 1929:695). Courtship activity in 1968 was most intensive during late July and August. This is compatible with the calving dates in 1969 based on the range in gestation periods.

## Pre-calving behavior

Pregnant cows were easily identified by distention of the abdomen. Figure 35 is a picture of the cow marked radio channel 7 taken on March 13, 1969 which illustrated this condition. The cow was obviously pregnant at that time although her calf was not born until the second week in July. Engelhard (1970:22) also found the distended abdomen to be the simplest indication of pregnancy. Egerton (1962:39-41) points out a sharp hollow between the abdomen and hind quarters, swelling of the udder, and swelling

and loosening of the vulva as indicators of pregnancy. While these characteristics were observed at Wind Cave, the **distention** of the abdomen was believed to be the best recognition of pregnancy as it allowed rapid evaluation of groups of cows and was practical at a distance when binoculars or a spotting scope were necessary.

Increased wariness of cows and resulting increase in flight distances have already been mentioned. Egerton (1962:41) noted an increased restless activity in cows up to 12 hours before calving. Engelhard's observations (1970:22) are similar to those at Wind Cave in that he noted a wariness in cows during May at the National Bison Range. As his study began in May, it is not possible to compare the wariness of cows in late March and April.

On April 9, 1969, a cow was observed moving away from a group at 1320 hours. The cow was holding her tail straight out from the body. She urinated once from an exaggerated squatting posture and then turned to sniff at the urine. I attempted to follow this cow on foot as this atypical behavior might have indicated initiation of parturition. The cow was moving rapidly, however, and visual contact was lost due to the terrain and the presence of timber. Neither tracking attempts nor a systematic foot search of the area revealed the location of the animal. As no calves were observed on the area until April 21, it was not believed that this animal gave birth to a calf at that time.

On April 25, 1969, another incident of a cow traveling alone was noted. The animal had a swollen vulva and distended abdomen. It was moving along in an irregular pattern while sniffing at the ground as if

trailing. Pursuit of this animal was not possible, but her unusual behavior merits mention here.

A decrease in group size prior to calving indicated a dispersion of cows at this time. As example, of 43 cow groups observed in April, 21 (48.8%) had fewer than 20 members. In contrast, only 3 (12.5%) of 24 groups observed in March had fewer than 20 members and only 2 (9.1%) of 22 groups observed in June after the peak in calving fell into this category. This dispersion caused problems in searching for parturient cows.

# Parturient behavior

In June of 1968, 216 hours were spent in the field searching for parturient cows. In 1969, an additional 552 field hours were recorded during the calving season. Despite this intensive effort, only one observation of birth of a calf was recorded. This limited success was undoubtedly due to size of the area, terrain, and wariness of cows during these periods. Even this one observation was not entirely complete as the actual birth of the calf was not witnessed but rather only the events immediately post-partum. Following is a description of the event.

On June 26, 1968, I was observing a group of approximately 150 animals located in a prairie dog town in the southeast corner of the park. The herd was loafing with few members standing. At 1210 hours MDT (midday), a cow on the periphery of the group stood up and a 3 foot long portion of afterbirth was observed hanging from the vulva. At her feet was a calf covered with bloody mucous material. The calf was wet all over and dark brown in appearance. The cow immediately began licking the calf.

1215: Cow continued to lick the calf.

1218: Cow observed ingesting extra-embryonic material clinging to the hind quarters of the calf. The calf made one weak attempt to stand.

1222: Cow continued licking the calf. The calf lying on its side with its head raised. Afterbirth still hanging from the vulva of the cow.

1224: Cow continued to lick the calf. The calf's hair now appeared woolly in nature. The calf made another attempt to stand.

1227: Calf made another attempt to stand as the cow continued licking it.

1230: Cow expelled about one-half cup of fluid from the vulva by obvious contractions. The afterbirth appeared to be hanging lower. The calf made another attempt to stand but fell back.

1231: A yearling bison just approached and licked the calf.

1234: Cow was still licking the calf. The group was now up and grazing.

1236: Calf observed nuzzling the face of the cow.

1239: Cow still licking the calf all over. The calf attempted to rise and managed to hold the hind quarters up for 27 seconds.

1242: Two yearlings and a 2-year old bull investigated the calf. The 2-year old sniffed the ground and gave a lip curl of 4 seconds (Note: the term "lip curl" will be discussed later with sexual behavior). Two cows, one with a calf was standing within 15 feet of the newborn calf.

1246: The calf lunged forward in an attempt to stand but fell on its nose. Now four cows and one calf in the vicinity.

1250 (40 minutes after first observation): The calf stood for 30 seconds but appeared quite wobbly. It fell when nuzzled by another calf.

Two cows in the vicinity jumped sideways when the calf fell and the mother began licking the calf.

1252: Calf up and standing. It took 3 wobbly steps.

1256: Calf still standing. The cow was still licking the calf and appeared to be steadying it. There's a portion of the umbilicus approximately 4 inches long still attached to the calf.

1258 (48 minutes after first observation): Calf appeared to be attempting to suckle. The calf began "searching" with its nose between the forelegs of the cow and proceeded backward along the abdomen, investigating as it went. The cow nudged the calf with its nose in the direction of the udder.

1301: Calf now suckling.

1305: Calf still suckling.

1308: Calf stopped suckling for a few seconds but resumed again.

1314: Calf still suckling.

1315: Calf still suckling. A group of coyotes just howled for 15 seconds to the southwest. The herd was becoming vocal with grunting from cows and calves.

1316: Calf now lying down with the cow standing over it. The group slowly started to move eastward with increased grunting from cows.

1320: The cow was still standing over the calf. The remainder of the group continued moving off to the east.

1322: The calf was standing beside the cow.

1326: Cow-calf group vocal and moving. The newborn calf was suckling again. Still wobbly in stance.

1330: Calf still suckling.

1335: Entire cow-calf group has moved away. The cow watched the group leave and appeared to be attempting to nudge the calf in the direction of the group using her nose.

1340: Cow still nudging the calf in the direction taken by the herd, but the calf is having difficulty in walking.

1348: Calf suckling again.

1350: The cow-calf group was now approximately one-quarter mile to the east of the pair. The calf lay down with the cow licking it.

1400: The cow-calf group has moved out of sight over a ridge. The calf appears to be sleeping with the cow standing over it.

1406: The calf is up and walking in circles.

1409: Calf lying down with the cow licking it.

1416: Eight cows with two calves have circled back from the cow-calf groups and are standing on a ridge 200 yards from the cow and calf.

1421: Cow standing quietly with the calf lying down.

1430: Calf still lying down with the cow grazing nearby.

1431: Cow lying down with the calf.

1445: Cow and calf standing with the calf suckling.

1500: Cow and calf lying down.

1515: Cow and calf still lying down.

1535: Cow and calf still lying down.

1540: The calf is now standing and nuzzling the cow about the face. The cow licked the calf about the head. The calf made one jump at the side of the cow.

1544: Cow stood up and the calf suckled.

1548: Calf moving in circles. Cow attempting to nudge it in the direction of the group. Calf now trotting with the cow following very slowly.

1554: Cow and calf now moved off in the direction of the group. The cow is following the calf and nudging it with her nose (Fig. 37).

1600: Cow and calf now in with the cow cow-calf group and lying down. 1700: Cow and calf still lying down.

Although this observation was the only one of its kind during the study, it does provide some basis for comparison with other studies. McHugh (1958:31) reported on the events included in and immediately following parturition. Egerton (1962:42-52) also reported on the birth of two calves. Engelhard (1970:22) did not witness parturition but did report seeing 8 cows "within a few minutes or hours after giving birth."

The observation of birth just described occurred when the cow was located on the periphery of a large cow-calf group. Some authors have reported that cows leave a group before calving (Grinnell 1904:132, Seton 1929:695, Soper 1941:391, and Egerton 1962:41). Others report that cows give birth to calves either when separated from cow-calf groups or when with them (Hornaday 1889:425, Roe 1951:98, McHugh 1958:31, and Engelhard 1970:22). Based on the observation discussed, the difficulty in locating parturient cows, and the dispersal of cows prior to the calving period, the situation at Wind Cave suggests the latter hypothesis. Schein and Fohrman (1955) indicate that shortly before and immediately after parturition, a domestic cow temporarily ceases to function as a member of

Fig. 37. Cow with newborn calf. This calf is approximately 4 hours old. The cow is following the calf and attempting to nudge it in the direction of the cow-calf group located one-quarter mile away. Approximately 4 inches of the umbilicus is still attached to the calf

Fig. 38. Bison calf suckling. This posture is the typical one for suckling. Calves assume this posture on either side of the cow

Fig. 39. Bison calf attempting to suckle from behind. This posture was typical if a calf was suckling in the parallel posture shown in Fig. 38, and the cow moved away. The calf would then attempt to suckle between the hind legs while the cow was walking



the herd. The cow observed at Wind Cave did not graze or move with the cow-calf group following the birth of the calf but did rejoin it within 4 hours.

McHugh (1958:31) reported that both cows observed in his study gave birth to calves while lying on their sides. Of the two cows observed in Egerton's study (1962:42), one was lying down and the other standing. The cow at Wind Cave gave birth while lying down.

The calf observed at Wind Cave made a weak attempt to stand within 8 minutes of the first observation but was unable to do so for 40 minutes. The calves in McHugh's study (1958:32) stood at 18 and 28 minutes following birth. Egerton (1962:45) reported calves attempting to stand in 3 minutes in one case and 6 in the other. One was successful in 10 minutes and the other in 20 minutes.

McHugh (1958:31) reported both cows licking the calves almost constantly for at least the first 10 to 25 minutes following birth and reported consumption of the afterbirth by both cows. Egerton (1962:45) commented that this licking by the cows stimulated the calves to move. She reported only one cow ate the afterbirth. The licking of the calf by the cow at Wind Cave was almost continuous for the first 29 minutes. The cow did not lose the portion of the afterbirth hanging from the vulva during the first day but was observed without it the next day. It is not known whether or not she ate this. Hafez and Schein (1962:278) stated that domestic cows lick the foetal membranes and fluids from the calf and usually eat the placenta and sometimes the bedding contaminated by foetal and placental fluids as well. Fraser (1968:117-8) stated that many ungulates remove the afterbirth from the birth site by eating it. He goes on to state that species which eat their afterbirths generally maintain their offspring close to the birth site for some days at least, while the ungulate species which do not eat their afterbirths generally lead their neonates away from the birth site very early in the post-partum period. He concluded from this that, as consumption of these membranes do not offer substantial gain, this behavior is a maternal adaptation of predation on vulnerable neonates. Although the evidence presented here is far from conclusive, this latter reasoning may not apply to bison.

Egerton (1962:46) observed that calves attempted to suckle as soon as they could stand. She noted a suckling motion in calves prior to standing. The calf observed at Wind Cave began suckling behavior within 8 minutes after it first stood up. Egerton also observed that calves first direct their suckling attempts to the neck region of the cow and then follow the belly with their noses. She did not mention the cow nudging the calf in the direction of the udder. Engelhard (1970:23) observed the calf of a tame cow in an enclosure during its first day and noted that the calf first went to the pectoral region and thrust its head underneath the foreleg of the cow before moving to the inguinal region and suckling.

Egerton (1962:48) noted that cows with new calves tried to prevent investigations of those calves by other bison by aggressive motions. Engelhard (1970:23) commented that the tame cow and three others observed on the open range did not seem to be bothered by these investigations. Although the cow observed at Wind Cave remained very close to her calf when other bison approached, she did not attempt to keep these animals away.

# Feeding behavior in calves

During the first week of a calf's life, suckling occurs frequently and at irregular intervals. Durations of suckling observed varied from a few seconds to a maximum of 21 minutes. Engelhard (1970:29) listed suckling duration as a few seconds to 15 minutes in day-old calves and 5-18 minutes in calves during the first week. Egerton (1962:82) was able to provide data on duration of suckling periods from seven calves in the Waterton herd. She reported an average of 6.6 minutes as duration of suckling during the first week. This does deviate significantly from her over 11 average over a 13 week period which was 6.7 seconds. Average duration is more meaningful in her study than at Wind Cave because she was constantly able to identify the individuals involved. Hafez and Schein (1962:265) pointed out that rate of suckling is related to milk available from the mother and persistence of the calf during suckling.

Suckling posture during the first week and throughout the nursing period is typically that of the calf standing parallel to the cow but facing in the opposite direction (Fig. 38). The calf flexes its head up to the udder and may frequently bunt the udder during suckling. The nursing cow frequently licks the calf in the perianal region and on the hips, especially during feeding periods in the first week of the calf's life. Engelhard (1970) and Egerton (1962) report basically the same information. Fraser (1968:136-8) points out that suckling postures are "typically those of open, upright stance in monotocous species and of recumbent extension in polytocous species." As bison are usually considered uniparous with twins being rare (Seton 1929, Garretson 1938,

Soper 1941, McHugh 1958, and Fuller 1961), this upright posture in bison supports Fraser's comments. Engelhard (1970:73) was able to observe twin calves born at the National Bison Range during his study and also described the upright stance as the suckling posture in these calves.

Although the posture just described is typical of bison calves from their first week on, a second posture was noted even during the early part of the calf's life. This posture was suckling from behind (Fig. 39). Typically, if a calf was suckling in the parallel posture and the cow moved ahead, the calf would shift its position to remain parallel. If the cow continued to move ahead, the calf might make attempts to suckle from the rear, reaching between the cow's hind legs with its head. Although this posture was most common when cows were moving, it was occasionally observed when cows were standing still. Engelhard (1970:73) reported one of the twin calves suckling in this posture while the other was in the parallel stance. Egerton (1962:84) also noted this as a suckling posture **typically occurring when cows were moving**.

Calves employ a behavior pattern to stop the forward movement in cows which Egerton (1962:86) calls "heading off." In this pattern the calf hurries alongside and in front of the cow and steps under the cow's chin, blocking her progress with its body. As soon as the cow stops moving, the calf continues on under the cow's chin and assumes the parallel suckling posture. If the cow starts to move again, the calf repeats the maneuver. This process continues until the cow stops and nurses the calf or until the calf is discouraged by a kick from the cow. The calf suckles on the opposite side of its approach to the front of the cow. This

pattern was quite common at Wind Cave, particularly when cows were moving during grazing periods. Egerton (1962:87) observed this heading off by a calf 45 minutes after it was born. Engelhard (1970:37) also observed this pattern.

Bison calves were observed engaged in grazing behavior during the second week of life. One observation in June, 1968 was of a calf 5 days old nibbling at vegetation as its mother grazed. Engelhard (1970:46) reported sporadic grazing activity by calves during the first 2 or 3 weeks. He commented on survival of calves deprived of milk and recorded an incident of a calf estimated to be 1 month of age which was accidently The abomasum of this calf was found full of partially digested killed. grass. Two bull calves estimated at 2 months of age were orphaned at Wind Cave as the result of the 1969 roundup. These calves remained together on the periphery of cow-calf groups throughout the fall and winter and appeared to thrive. No evidence of fostering of these calves by cows was observed. Also, on August 23, 1969, a 7-week old calf was separated from its mother during a stampede (Note: This stampede was started intentionally for a film crew on the area. Bison were never observed to stampede except when harassed.) The mother of this calf had been observed for 5 weeks as being emaciated, and apparently she was unable to take flight with the other animals. This calf was also observed to survive without a foster cow. Engelhard (1970:79) did report one incident of fostering of an orphan calf by a cow with a calf of her own.

This brings up the question of how long calves suckle and how weaning occurs. Engelhard (1970:57) suggested that the weaning process begins

during the rut when cows become less tolerant of suckling attempts. McHugh (1958) observed cases where calves were seen with their mothers for over a year. He also observed eight instances of yearlings suckling and found the duration between 2 and 8 minutes with an average of 4 minutes. Egerton (1962:91-3) also observed instances of yearlings suckling and stated that it is "usual for bison calves to suckle until they are 9 months old, and in some cases yearlings continue to nurse if their mothers do not have new calves."

At Wind Cave, 21 instances of yearlings attempting to suckle were observed. In 13 of these instances the cows involved had calves of the year. On only three occasions were these attempts successful when the yearlings were observed to suckle for periods less than 1 minute before the cow moved on. Yearlings attempting to suckle used the heading off pattern, but cows responded by turning with the yearling instead of allowing movement to the udder. On July 24, 1969, one atypical observation of a 2-year old bull following a cow and attempting to suckle from behind was noted. The cow continued walking and kicked at the bull with her hind leg when he tried to bunt her udder. The bull did have some success, however, in that milk was observed on his nostrils. This incident lasted 1 minute and 15 seconds.

Fraser (1968:160) points out that the process of weaning is a poorly understood phenomenon. Before weaning, the young animal must have adapted to feeding behavior which it will retain into adult life. Perhaps, as some authors suggest, the initial weaning process begins during the rut. However, in view of the fact that bison calves continue even after the

breeding season, there must be additional mechanisms involved. I believe that the increase in size of the calf and the increased strength with which it bunts the cow may play an important role in weaning. As calves get larger they must bend the head down further to suckle (Fig. 40). The cows appear to be less tolerant of the vigorous bunting which calves continue to use as they get older. Even the heading off behavior of the calf will not always induce a cow to stand as the calf gets older. Calves 4 to 5 months old were observed bunting the cow so hard that the cow was lifted off her hind feet. Instead of standing as observed earlier in the year, cows bunted in this manner moved away from the calf. Persistence of these older calves often resulted in the cows kicking at the calves with their hind leg or circling around the calves to prevent access to the udder.

Finally, the drinking behavior of the calf resembled that of the older bison. Calves were observed drinking from ponds in their second week of life. Initially, calves just waded a short distance out into the water (Fig. 31). With increasing age, however, the calves moved into water belly deep, just as other bison do. Calves were observed to urinate upon entering water as older bison do.

### Cow-calf bonds

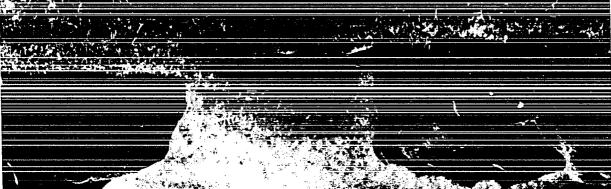
During the first week of the calf's life it remains very close to the mother cow. It spends a great deal of time lying down during this early period. Usually the calf aligns itself so that it is facing the cow at this time (Fig. 41). During the first days of its life it does not wander beyond a distance of about 25 feet from the cow. Egerton (1962:53)

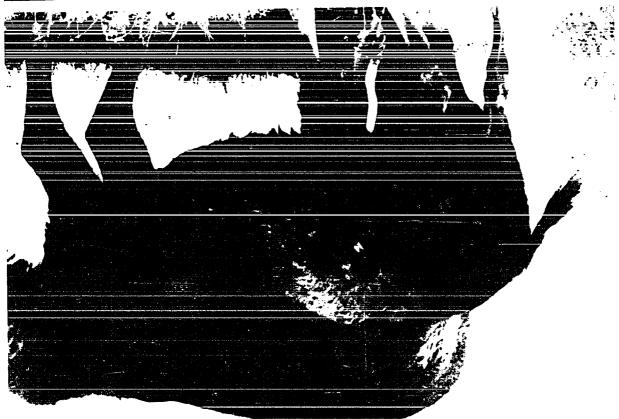
Fig. 40. Three-month old bison calf suckling. Calves of this age and older must bend the head down further to suckle than younger ones. Cows appear to become less tolerant of the vigorous bunting of older calves during suckling

Fig. 41. One-week old bison calf facing the cow. Calves at this age usually align themselves in this manner so that they are always facing the cow

Fig. 42. Bison calf lying down. Calves first drop to their knees and fold the rear legs under them. Then they lower themselves to the ground. In standing up, the process is reversed







observed that cows graze in a circle, semi-circle, or horseshoe pattern around calves which are lying down. This was not noted in the Wind Cave herd nor in the herd studied by Engelhard (1970:30).

Engelhard (1970:31-4) described a "bonding period" between a cow and newborn calf. He stated that cows separate themselves and their calves from other members of the group to "learn" to identify each other by means or "sounds (vocal, breathing, body movement), sight (color, shape, body positions), feel (bodily contact during nursing and licking by the mother), and smell." He further stated that by these means the calf "imprinted" on its mother at a very early age, facilitating survival until weaning. At Wind Cave, an intimate relationship was noted between cows and their calves shortly after the birth of the calf, but no actual isolation such as Engelhard described.

Calves roamed farther from their mothers during the third week of life. Distances ranged up to 50 yards. These separations were especially obvious when cow-calf groups were actively grazing. Any stimulus such as intrusion of a vehicle, however, caused the cows to begin grunting and calves to run to their mothers. Such instances always caused calves to begin suckling. As a general statement, disturbance almost always caused the calf to begin suckling. I have noted similar suckling behavior in young of domestic animals such as cattle, horses, and cats.

Vocal communication by grunting was noted by McHugh (1958:33). He noted increased vocalization (1) by a cow when her calf strayed away; (2) by a cow during moments of danger, such as the approach of a strange animal or object; (3) by a calf when its mother strayed away; (4) by

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either the cow or the calf when one was separated artificially from the other; (5) by cows or calves during herd movements, with a distinct increase in grunting synchronized with the movement; (6) by cows when a wide river was to be crossed; (7) by either in answer to the other; and (8) by either prior to nursing. All of these situations were observed during my study at Wind Cave with the exception of grunting during a river crossing as no river flowed through Wind Cave. In all of these instances the cow and calf came closer together as a result of the vocalization.

Two interesting situations occurred during my study which demonstrate the change in cohesion between cows and calves with increasing age in the calves. Following is a description of those observations.

On April 18, 1969, a group of 61 bison were observed moving through an open gate in a wing fence. I moved the study vehicle to the middle of the gate, effectively cutting off 10 animals from the remainder of the group. There was a clearance of 12 feet on one side of the vehicle and 15 feet on the other which allowed the bison to pass by. The author made no attempt to frighten the animals but sat in the vehicle to observe what would happen.

Within 3 minutes, 4 adult cows, a 2-year old bull, and a 3-year old bull all passed by the vehicle. The animals approached cautiously and ran past but slowed to a walk after passing the vehicle. The remaining four animals were all yearlings (calves of the previous year). All four of these animals began grunting loudly at a frequency of about one grunt per second. One of the cows that had passed through the gate turned and looked at the four but continued on her way.

The yearlings began running up and down the fence grunting loudly. The group of bison that had passed through continued to move away with no members answering the grunts of the yearlings. Finally, 26 minutes after being separated, the yearlings passed the vehicle one at a time. All four ran to join the group which was one-half mile away by this time.

In contrast to the above situation, I had the opportunity to separate members of a cow-calf group on June 21, 1969. The location and conditions of vehicle placement were the same. The group involved 80 adults and juveniles, with 25 calves. The group was about half through the gate when the vehicle was moved into place.

One cow and calf passed by the vehicle with the calf very close to the mother. Another calf was separated from its mother by the fence. These two animals both began grunting loudly and running up and down the fence on opposite sides. The pair continued this activity for 13 minutes until the calf finally ran past the vehicle and rejoined its mother. The calf began suckling immediately.

The remainder of the group which had not passed through the gate was running up and down the fence grunting. Another cow, apparently separated from her calf, ran along the fence on the opposite side. Finally, one of the cows in the group ran through the gate but immediately circled back to the fence on the opposite side and joined the cow already there. Both cows continued to grunt in answer to the grunts from the separated group. Two calves in the separated group moved close to the fence. They began running up and down with the cows on the opposite side. One of the calves tried to run through the fence three times. The cows involved appeared to

be attempting to "lead" the calves to the gate as they would run along the fence with the calves toward the gate. If the calves turned back, the cows would drop back and grunt until the calves again moved toward the gate. All four animals were excited and breathing heavily with their mouths open. Finally the two cows came within 25 feet of the vehicle and stood grunting. After some hesitation, the calves ran through the gate and began suckling immediately. One of the calves was observed to have cut its nose slightly as a result of having run into the fence.

These two situations illustrate the decreasing bond between the cow and the calf as the calf gets older, particularly the decreased attention afforded by the cow. They also demonstrate how the cohesion between the young calf and the cow affect the movements of the cow and therefore the cow-calf groups. In the situation involving calves approaching 1 year, the group continued to move despite the distressed calls from these calves. In the group where the calves were one-month old and younger, the distress of the calves caused a change in the movement of the cow-calf group in that the group did not continue moving until the calves were reunited with their mothers. McHugh (1958), Egerton (1962), and Engelhard (1970) all noted a similar pattern.

### Calf postures

Bison calves spent a great deal of time lying down during the first month of life. Engelhard (1970:38) described the manner in which calves did this. He noted that calves first dropped to their knees and folded the rear legs under them. This same pattern was observed at Wind Cave (Fig. 42). Calves reversed the process when standing up.

Engelhard (1970:38) also described the typical postures assumed by calves while lying down. They include (1) head erect and looking around; (2) head set against the foreleg with the chin on the ground; (3) head extended forward from the body with the throat area and chin on the ground; and (4) head slung back and resting on the shoulder with the eyes closed. All of these postures were observed at Wind Cave with the last being the most unusual. It was observed, however, as illustrated by Fig. 43.

Calves were observed lying on their sides for long periods of time. In adult bison, the longest observation of an animal lying on its side was 4 minutes and 35 seconds by an adult bull. Calves were observed in this position for 30-40 minutes. The relatively short duration of this posture in adults may reflect discomfort caused by inefficient ventilation for passage of rumen gasses through the nostrils. The calves' diet of milk may not result in as much gas production as occurs in adult animals.

Egerton (1962:14) described a posture in bison which she termed the "gape." This pattern closely resembles a yawn but differs in that the animals do not breathe while showing this behavior. The posture is not common and was noted by Egerton primarily when a calf's mother or other bison sniffed the calf soon after birth. This pattern was observed infrequently in calves at Wind Cave (Fig. 44). The significance of the gape is not known.

## Play Play

Scott (1962:6) points out that in some species the development of behavior patterns depends on the opportunity for play and social contact.

Fig. 43. Bison calf resting. This posture with the head slung back and resting on the shoulder with the eyes closed was assumed by calves during **loafing** periods. Other postures such as seen in Fig. 41 were more common

Fig. 44. The "gape" posture. This pattern closely resembles a yawn but differs in that the animals do not breathe while showing this behavior. This posture is not a common one, and the significance is not known

Fig. 45. Calf group. Calves frequently formed groups such as this one during their first month. Activities in these calf groups are best defined as play



This play consists of immature forms of adult patterns and also functions to develop muscular strength through exercise. Egerton (1962:70) discusses the significance of play activity and indicates that it provides young animals with opportunities for group interaction, allows the animal to become familiar with its environment, and provides practice of behavior patterns which will be important in adult life. Whether or not these theories encompass all the reasons for play behavior in young animals, it must be recognized that this type of activity is quite common and undoubtedly functional.

During the first month of life, bison calves begin to spend some time away from the cows and frequently form groups with other calves (Fig. 45). These groups varied in size at Wind Cave from 2-9 members. Engelhard (1970:47) reported groups of 2-15 at the National Bison Range. Both at Wind Cave and in Engelhard's study, these groups were loosely organized and broke up when member calves moved to their mothers.

Activities in these calf groups are best defined as play. Egerton (1962:57) points out that it is "characteristic of the play of animals that it is recognizable as such, and people will agree that an action is play, even though they may be unable to explain why they interpret in such a way." She further states that the animals themselves "know that they are playing" by certain signals such as bucking and galloping around with the tail raised.

Play activities in bison calves include chasing each other, mock battles, and mounting behavior. In addition, calves were observed bucking and running in a bounding gait in which all four feet strike the ground at the same time much like the gait of mule deer (Odocoileus hemionus).

The bucking and bounding gaits were also observed in adult and juvenile bison, particularly on cool, crisp days. Even mature bulls were observed frolicking using these gaits on seven occasions. This bounding gait was also used by some bison when they were released from the corrals following handling operations.

Bison calves also played with yearlings and occasionally 2-year old bison. Calves did not yield in butting and pushing contests with these older animals unless the larger animals continued pushing the calves backward. On those occasions the calves broke off the play and returned to their mothers.

In addition to play interactions, bison calves ran and frolicked by themselves. One typical pattern observed during the hot summer months frequently took place when calves were lying down during loafing periods. The calf would suddenly jump up and run in circles or figure-eight patterns around the cow and other members of the group. These patterns usually took the calf in a 50 yard radius around the cow. Suddenly the calf would flop down and shake its head vigorously. This pattern might be repeated as many as four times in rapid succession until the calf was panting heavily. It appeared that the calf may have been responding to insect pests around the head when engaging in this activity. However, as that is only speculative, the activity is included in play behavior.

Mounting and mock battles usually accompanied each other. Two calves (or juveniles, for that matter) engaged in mock combat might break off with one member attempting to mount the other. The mounting animal would clasp the other and bounce along on its hind legs as the other animal ran

ahead. In one observation, two yearlings engaged in this activity and the mounting animal retained its position for a distance of approximately 45 yards before releasing its grasp. McHugh (1958:7) also reported this coupling of mounting behavior and battling.

Play mounting was practiced by both sexes. In bull calves the penis was not unsheathed and thrusting actions were very rare. In juvenile bison bulls, the penis was unsheathed and the thrusting actions accompanied the mount. Even adult cows were observed mounting other animals, although this was not nearly as common an observation as the mountings of calves and juveniles.

# Sexual Behavior

The term rut is used here to indicate the period during which bison engage in breeding activities. Fraser (1968:86) states that, in behavioral terms, each rut is like a dramatic puberty. The associated behavior reflects changes in endocrine balance with normal variation from one animal to another. Not all males will respond equally to testosterone output, nor will all males secrete equal amounts of that hormone. Therefore, not all males will show sex drive to an equal degree. The term "rutting behavior" generally refers to behavior of male animals.

# Sexual maturity in bulls

Sexual maturity in cows has already been discussed. Fuller (1961: 288) states that the situation in males is essentially the same as in females. That is, a small proportion of males attain sexual maturity as yearlings, about one-third as 2-year olds, and probably all 3-year olds

and older are mature. He studied sperm smears from 20 young males and recorded 1 of 6 yearlings, 3 of 8 2-year olds, and all 6 3-year olds had abundant, apparently normal sperm. Smears from the epididymides of 21 bulls culled at Wind Cave in October, 1968 were examined in the same manner. The results were 2 of 6 yearlings, 5 of 6 2-year olds, 4 of 5 3-year olds, all of 3 4-year olds, and the only 5-year old had abundant sperm present. These figures reflect a somewhat higher incidence of abundant sperm in yearlings and 2-year olds than that found by Fuller, but the small sample size in each study prohibits general statements.

# The "lip curl" posture

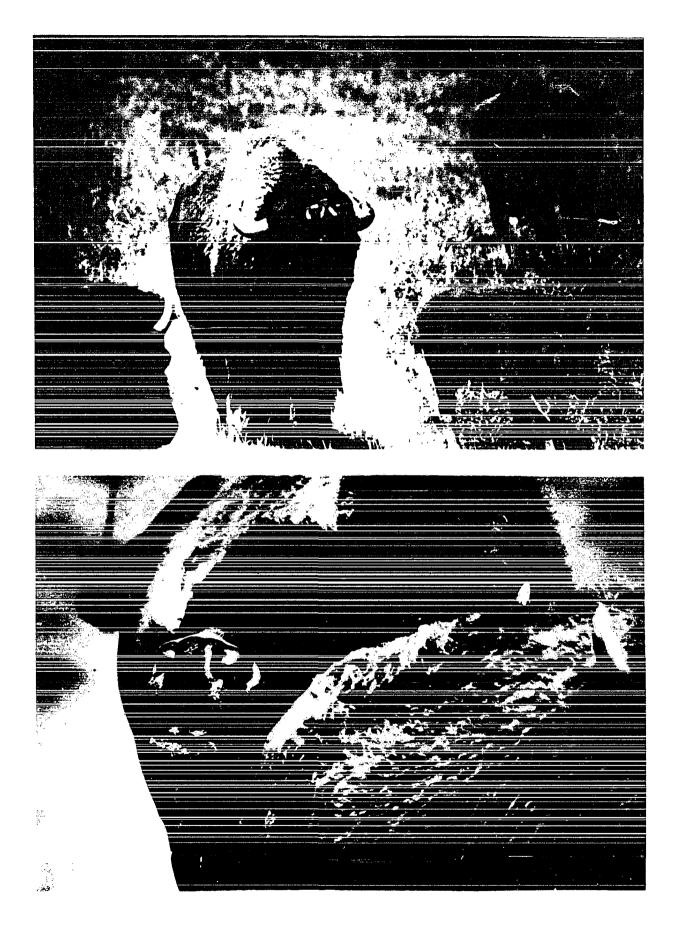
Fraser (1968:11) stated that there is mounting evidence that olfaction is fundamental in the stimulation of reproductive responses throughout very many ungulate species. He cites as evidence of this the variety of essentially similar olfactory reflexes exhibited in most male ungulates. He further states that this olfactory reflex was first termed "Flehmen" by Schneider (1930). McHugh (1958:24) described this posture in bison as "sniffing and extending neck with upcurled lip." Egerton (1962:16) termed this the "lip curl" in bison. Herrig and Haugen (1970:253) described this posture in their study at Ft. Niobrara. Engelhard (1970:68) also described this posture in bison but preferred the term "flehmen," considering "lip curl" misleading and nondescriptive. Although the two terms obviously refer to the same posture, the term "lip curl" will be used here following Egerton's precedence in bison literature.

The posture of the lip curl entails the animal extending the neck and turning the head upward (Fig. 46). The mouth is opened and the nostrils

Fig. 46. Lip curl posture. The bull in the photo is exhibiting the lip curl posture after sniffing the ground where the cow in the left foreground urinated

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Fig. 47. Lip curl posture. The bull shown in Fig. 46 is seen here exhibiting the lip curl posture after sniffing and licking the vulva of the cow shown in that figure



flared. The eyes are partially closed and rolled back. The posture is always preceded by sniffing activity--either on the ground or another animal. Also, the extension of the neck may involve one smooth movement or a rapid, single nod terminating in the extended position. Duration of lip curls observed at Wind Cave varied from 3 to 19 seconds, depending on the situation. The usual duration in adult bulls was 9-10 seconds.

The complete significance of the lip curl is not known. The most obvious explanation involves its increase in frequency by adult bulls during the rut. As example of this increased frequency, a 1-hour count of lip curls in a group of 75 bison during an afternoon grazing period on March 10, 1969 recorded 6 lip curls. A comparable count on 80 bison made on August 6, 1968 during the peak of the rut yielded 53 lip curls, 42 of which were by bulls 3 years and older.

Lip curls are generally associated with investigating of urine. Fraser (1968:11) suggests that the effect of urine on bulls during the rut may be one of recognition of approaching oestrous in cows. It is known that urine can carry breakdown products of hormones, including reproductive hormones. Fraser states that it is reasonable to assume that oestrous cycle phasing may be recognizable to the male by odor testing of urine from the female. Lip curls by bulls during the rut occur when the bull sniffs the ground where a cow has just urinated (Fig. 46) and following sniffing and licking the vulva during investigation of cows (Fig. 47).

This explanation is adequate for the increased frequency of lip curl behavior by bulls during the rut, but it does not completely explain the

behavior pattern. Bison of both sexes and all ages (except calves during their first week) were observed giving lip curls under varying circumstances. One cow was observed to urinate and then turn, sniff the ground, and give a 7-second lip curl. A yearling bull gave a 4-second lip curl when it sniffed at human urine on the ground. Although urine was the usual stimulus for lip curls, cows on three occasions were observed to sniff the perianal region of yearling bulls and present lip curls. Also, when bison were shot during the 1963 and 1969 culls, other members of the group approached the downed animals and sniffed at blood on them or on the ground and exhibited lip curls.

Multiple lip curls were observed on several occasions. These entailed bulls investigating cows, giving lip curls, continuing the investigation, and giving one or two successive lip curls. In situations such as these, the second and third lip curls were of shorter duration.

Bulls during the rut also were attracted to the area of a cow when she was urinating. These bulls usually placed their noses in the urine stream and then presented a lip curl. On three occasions calves estimated at 1 month old also placed their noses in the urine streams from cows and gave lip curls, 2 of 6-second duration and one of 7 seconds.

### Investigatory behavior

Rutting behavior began in June of both years and continued through mid-September. Sexual behavior was most pronounced in late July and all during August. McHugh (1958:23) observed the rut at Wind Cave from June 13 to September 14. The beginning and end of the rut are defined primarily by the initiation and subsidence of investigatory behavior among

bull bison.

Bull bison investigate cows by sniffing and licking the vulva region. This is usually accompanied by a nuzzling of this region by the bull. Such investigations are nearly always followed by a lip curl.

Fraser (1968:60) suggests that this genital stimulation by a male may have an effect on oestrus in the female. He cites experiments in cattle where artificial stimulation of the genitalia of cows induced oestrus in 31 of 32 animals within an average of 8 days. In another experiment in which electrical stimulation of the genitalia of anoestrous cows was used, 50% of the animals came into oestrus as compared to 5% of a control group. While I know of no similar experiments with bison, it does not seem unreasonable to suggest that this exogenous stimulation of cows by bulls may be instrumental in bringing on an oestrus condition.

In 1968, the first investigation by an adult bull in a cow-calf group was observed on June 21. The first roar from a bull investigating was observed on June 12. By June 20 of that year, mature bulls were moving in and out of cow-calf groups investigating cows. Typically these bulls moved through cow-calf groups investigating several of the cows. The bulls snorted while walking and showed an excited condition by elevation of the tail (Fig. 48). If other bulls were already in the group, various agonistic displays were observed.

A typical encounter was observed on June 27, 1968. The author was observing a group of 42 cows, calves and juveniles. At 0845 hours a bull estimated at 10 years of age was observed walking towards the group. The bull was snorting and wagging its head back and forth as it walked. The

Fig. 48. Adult bull moving through a cow-calf group in June, 1968. The bulls move into these groups at this time and begin investigating cows. The elevated position of the tail indicates an excited condition

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Fig. 49. Bull tending cow. The tending bond is characterized by a bull remaining with a cow for a period of time during the rut and attempting to keep the cow separated from other members of the group

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bull moved into the group with its tail slightly erect. A group of 5 2-year olds were standing on the periphery of the group watching the approach of the bull. When he was within 15 feet of these animals they jumped out of his path. The bull continued into the group and proceeded to investigate 10 cows, giving lip curls after each investigation. Then the bull stood within 20 feet of a 2-year old cow and began grazing.

At 0915, another bull was observed in the distance approaching the same group. This bull, also approximately 10-years old, approached within 500 yards when the bull already in the group began roaring and wallowing. The approaching bull answered the roars and stopped to wallow. Then it continued towards the group and stopped to wallow three more times. Both bulls continued to roar. The second bull moved into the group and investigated six cows, also giving lip curls after each. The bulls continued to roar, and the first bull wallowed two more times. Finally the second bull approached within 20 feet of the first and stood parallel to him but facing in the opposite direction. Both bulls continued to roar loudly and paw and horn the ground. This activity went on for 10 minutes before the first bull moved to another position on the other side of the group. The bulls roared back and forth sporadically throughout the morning and afternoon.

During July and August, bulls tended to remain with the cow-calf groups rather than to wander in and out of them. During this time roaring and wallowing activity increased until, during periods of high excitement, the roars were continuous and the wallowing caused so much dust to rise that the groups were partly concealed by clouds (Fig. 23).

The rutting behavior continued into September, but large adult bulls began moving out of the cow-calf groups in late August. At that time, younger bulls including 3-, 4-, and 5-year olds continued the investigatory behavior. September 9 was the first day following the rut in 1968 on which no courtship activity was observed. No day without this activity was recorded in 1969 until September 24. These dates marked the end of continuous rutting behavior. However, even after these dates a few instances of courtship were observed when bulls came in contact with cow-calf groups.

## The tending bond

Fuller (1961) agrees with Seton (1929) that bison are polygamous, or, more precisely, polygynous. McHugh (1958:24) states that the mateship in bison is one of temporary monogamy. By this he implies that bulls are promiscuous but that cows are served by only one bull. He describes the bond between the bull and the cow during the rut as a tending bond. Hafez and Schein (1962:266) note a similar pattern in domestic cattle and refer to it as "guarding" of the female by the male.

The tending bond is characterized by a bull remaining close to a cow for a period of time. During this relationship the bull attempts to keep the cow separated from other members of the group. When walking or standing, the typical position is with the bull parallel to the cow and facing in the same direction. The bull is positioned slightly back so that its head is about even with the cow's shoulder (Fig. 49). When bulls are tending cows that are lying down, the bull may lie or stand very close to the cow (Fig. 50).

The duration of the tending bond is variable. The longest duration noted at Wind Cave was 8 hours when a group was under observation the entire time. Bonds probably were of longer duration, but this could not be tested without better identification of individuals. Egerton (1962: 115) states that tending bonds last for minutes, hours, and sometimes several days.

During a tending bond, bulls demonstrate intolerance of other group members of either sex, but particularly of adult bulls. This intolerance is expressed by roaring, wallowing, threat postures, and occasionally combat. During the entire study, however, bulls were never observed making aggressive actions towards calves of cows being tended. The calves did, however, move out of the way of approaching bulls. Tending bonds were frequently disturbed by the approach of other bulls which caused the preceding bull to move off. These encounters, in the absence of combat, lend support to the idea that some dominance mechanism was at work.

Oestrus in bison cows is detected by conspicuous swelling of the vulva so that the red mucosa is exposed. This is usually accompanied by slight elevation of the tail. Cows with these symptoms were most actively tended and defended by bison bulls. The cow in Fig. 50 exhibited both of these symptoms of oestrus. Schein and Fohrman (1955) indicate a further symptom of heat in cattle is a tendency to mount other cows. This was observed on only three occasions in bison at Wind Cave.

Tending bonds early in the rut involved primarily cows without calves, i.e. 2-year olds. Herrig and Haugen (1970:255) noted this same pattern at Ft. Niobrara. Fuller (1961:288) demonstrated that foetuses

Fig. 50. Bull tending cow. When cows are lying down, tending bulls lie down very close to them or stand over them as shown here

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Fig. 51. Elk calf. This calf was harassed by bison on June 3, 1969. Although the bison hooked at the calf and tossed it into the air, the calf did not have external injuries when examined

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carried by lactating cows were significantly smaller than those carried by non-lactating cows. He suggested from this that cows accompanied by calves breed later. Assuming cows tended early in the season are bred before cows tended later, the observations of tending at Wind Cave and those by Herrig and Haugen agree with Fuller's findings.

## Mounting behavior

During the periods of June-September for 1968 and 1969, a total of 1,572 hours was spent in the field searching for and observing bison. During this time, 196 cow-calf groups were observed. Despite this effort, complete copulation was never observed. Several sightings of copulations were reported by personnel not on the project, but due to the frequency of these reports and the lack of observations through concentrated effort, I believe that at least the majority of these reports were of false or attempted mountings. Garretson (1938) points out that copulation in wild bison is rarely seen by the human observer. He and Fuller (1960) have suggested that this is because copulation occurs most often at night. Egerton (1962:116) also reported not having witnessed complete copulation.

Herrig and Haugen (1970:256) describe one observation of copulation. This occurred at dawn. The bull attempted to mount the cow eight times and was successful on two attempts. After these attempts, the cow would not allow the bull to remount and the two began grazing. The bull remained with the cow the remainder of the day but was observed with another cow on the following day.

Although no complete copulations were observed, numerous "false" mounts were witnessed. Fraser (1968:100) indicates that false mounting is

commonly seen in male ungulates. He reports that false mounts in horses usually precede an effective one, but this was not the case with the bison at Wind Cave. False mounts differ from successful copulations in that there is no intromission of the penis in the former and the cow refuses to stand for the bull.

"Chin-resting" is noted by Hafez and Schein (1962:267) as an activity preparatory to mounting. They report that non-receptive female cattle respond to chin-resting by escape and avoidance, while those in oestrus respond by standing to be mounted. Fraser (1968:98) also includes this as an important part of mounting behavior.

In bison observed at Wind Cave, the chin-resting behavior might better be described as a "head throw." A bull tending a cow frequently would swing his head onto the back of the cow and attempt to mount. During the activity, the bull would exhibit a partial erection. Also, this activity was always preceded by a series of three or four rapid, soft-sounding, snorts resulting in a panting sound. In all instances observed, the cows moved ahead and the bulls resumed tending. McHugh (1958:29) also described this behavior and believed the short panting sounds forewarned the cow of the attempted mount.

Although complete copulation was never observed, evidence of cows having been bred was seen. This was noted when cows were seen holding their tails in the air and curled off to the side. The cows stood in a hump-backed posture for as long as one hour. Twelve observations of these postures were made. In one of these observations the cow was observed to void a milky urine. McHugh (1958:29) indicates that this occurs right

after copulation. The cow was being tended by an 8-year old bull at the time, but no subsequent mounting was observed.

Another indication of copulation is breeding wounds high on the flanks and posterior half of the backs of cows. The cow in Fig. 41 has obvious breeding scars from these wounds. These wounds are the result of blows from the front hooves of bulls in mounting (McHugh 1958:30). At first I believed that the frequency of these wounds could be used as an indicator of breeding frequency. However, it was soon discovered that cows lick these wounds during grooming activities and thereby keep the wounds open. The cow designated as radio channel 7 was observed with these breeding wounds during the last two weeks in August. The best indication of copulatory activity derived from these wounds (skin scrapes) is that by mid-August of both years, approximately two-thirds of the cows observed showed evidence of mounting wounds received during the breeding season.

## Chase behavior

During late July and August of both years, behavior patterns described as "clases" were observed. These occurred when a cow being tended by a bull began running in a circle or figure-eight pattern. These patterns ranged in size up to one-quarter mile in diameter. In these chases the bull tending the cow would run alongside or behind the cow, usually roaring. Other bulls in the vicinity along with cows, calves, and juveniles usually joined in by running in a column formation behind the lead pair. During these periods of high excitement roaring increased, particularly from the bulls involved in the chase.

If timber was present in the area, the cow would frequently run in among the trees followed by the rest of the group. In this manner these groups disappeared for as long as 10 minutes before reappearing. It is possible that copulatory activity may have occurred during these periods when the groups were out of sight. On one occasion in August of 1968, three of these chases were in progress simultaneously. This resulted in high excitement in the cow-calf group being observed. It is possible that these chases may function as dispersal mechanisms to alleviate arena behavior prior to copulation and thereby diminish combat encounters.

#### Masturbation

McHugh (1958:30) reports four occasions when bulls were observed to unsheath the penis, move the hind quarters as though thrusting in copulation, and ejaculate. Hafez and Schein (1962:269) report that this is common practice in domestic bulls. They cite some evidence that this may be related to high protein in the diet.

On June 28, 1968, a bull was observed in a posture which might have suggested masturbating activity. At 0942 hours, a 5-year old bull was observed standing next to a pond. The bull sniffed the ground and assumed an exaggerated hump-backed position. The bull had a full erection for 5 seconds. Only slight thrusting movements were observed and no ejaculation.

# Interspecific Relations

The relationship between the bison and prairie dogs has already been discussed. Other observations made during the study provide information

about the relationships between bison and other animals on the park. This section obviously cannot include all the intricacies of these ecologic relationships, but descriptions of notable observations are worthy of attention.

## Bison and elk

During the course of the study, the elk population at Wind Cave consisted of approximately 800 animals. As elk are predominantly grazers, they share feeding habitat with the bison (Koford 1958:69). Crepuscular feeding behavior by the elk minimized encounters between the two species. However, three events recorded during the study indicate some conflict between bison and elk.

On June 8, 1968, Gayle Herbert, Fire Control Aid on duty in the Rankin Ridge lookout tower called park headquarters and reported bison harassing an elk calf. The report was received at 1900 hours, and two park rangers and I went to the area to investigate. Mrs. Herbert reported that five bull bison on the periphery of a cow-calf group moved from the group to an cow elk and her calf. The bulls became quite excited and began circling the calf and hooking it. The cow elk attempted to lure the bulls away from the calf but was unsuccessful. Mr. Herbert, in the tower with his wife and also a witness to the event, stated that at one time the calf was thrown approximately 10 feet into the air by one of the bulls. After about one-half hour, the calf did not move and the bulls moved off.

The two rangers and I found the elk calf where it had been attacked, approximately three-quarters of a mile from the tower. By this time,

darkness had set in and a heavy rain was starting. The calf was found lying on a hillside where the bulls had left it. It was still alive, and there was no evidence of external wounds. When lightning flashed, a cow elk could be seen standing on a ridge about 300 yards away. The calf was carried out of the rain to a nearby pine tree. It bleated weakly while being carried. When placed on the ground, the calf jumped up and trotted off in the direction of the cow with a wobbly gait. The animals were not observed again, and a search of the area the next day yielded no observations of a cow elk with a calf.

On June 3, 1969, Mrs. Herbert was again on duty in the lookout tower and reported a similar incident. The call was received at 0610 hours and Dr. Arnold Haugen and I left for the tower immediately. According to Mrs. Herbert, an elk calf, apparently born during the night, was harassed by a group of bison including cows and calves. The bison moved into the area about 0545 hours. Some bulls in the group roared as during the rut when they came in contact with the calf. They hooked and tossed the calf with their horns as in the previous observation. Mrs. Herbert said it looked as if the bison cows attempted to lick the calf. One 2-year old bull attacked the calf in the same manner as the older bulls. During these attacks the elk calf was moved about one-quarter mile. During the attacks a cow elk circled the bison group but did not attempt to rescue the calf. The bison apparently left suddenly and moved away from the area.

The calf was located and examined. It was found lying in grassland where the bison had left it (Fig. 51). There was no evidence of external

wounds or broken legs. The calf did not move when examined. The calf was left in that position. Mrs. Herbert observed a cow elk with a calf in the vicinity the next day. I searched the area where the calf had been located and could not find it.

On June 28, 1969, Mrs. Herbert witnessed eight bison bulls harassing a large bull elk. The bison butted the elk which they had cornered. The bulls left the elk lying down. As the incident occurred at 1900 hours, the length of time that the elk remained is not known. The area was searched the next day but the animal was not found.

In some situations these observations might be questioned despite the fact that the elk calves were located on both occasions. However, both Mrs. Herbert and her husband are trained observers with many years of experience on lookout towers in the area. Also, both were very interested in the bison research and were of great assistance on numerous occasions. The author has every confidence that the observations were accurate.

#### Bison and predators

Few predators are capable of taking bison. Fuller (1960:15) reports that the wolf (<u>Canis lupus</u>) is the only known predator of bison at Wood Buffalo National Park. Roe (1951:155) and Garretson (1938:72) agree that there is little doubt that the most important predator of North American bison was the wolf. Gard (1959:20) reports that the grizzly bear (<u>Ursus horibilis</u>) and the mountain lion (<u>Felis concolor</u>) also occasionally prey on bison. None of these major predators were present at Wind Cave. (Note: Infrequent sightings of mountain lions were reported but were not verified and are probably questionable).

Probably the only predator capable of taking bison at Wind Cave would be the coyote (<u>Canis latrans</u>). Soper (1941:389) states that some people believe the coyote capable of preying on bison, but he does not regard them seriously due to their size. No evidence of coyote predation on bison was ever observed at Wind Cave, although coyotes were commonly seen and heard. Two interactions between bison and coyotes were recorded.

On March 10, 1969 at 1530 hours, I observed an adult bull bison running over a hill with three coyotes following. When the bull dropped over the hill, the coyotes stopped running and began sniffing in the grass. When I approached within 400 yards, the coyotes took flight. At this time it was observed that there were five more bison bulls over the hill which group the first bull had joined. The coyotes ran within 50 yards of these bulls when fleeing from the author. This caused the bulls to turn and run in another direction. Although it was obvious that the coyotes "bothered" the bulls, it is questionable if the three would have been capable of downing one of the mature bulls.

On July 16, 1969, I was observing a group of 67 adult and juvenile bison with 21 calves at 0455 hours. It was drizzling rain and the wind was calm. A group of four pronghorn does with a pair of twin kids was lying down within 200 yards of the bison. A coyote approached from the west of the groups. The four does first observed the coyote and moved in its direction. The coyote ran from the does when they were within 25 yards and moved towards the bison group.

A yearling bison in the group chased the coyote for a short distance. As the coyote moved through the vicinity of the bison, adults and

juveniles would move toward it with their tails slightly erect when the coyote was within approximately 20 yards. The coyote ran from these animals but continued to circle around and approach others. It finally moved away from the group and circled around behind me.

At 0525, the coyote managed to single out the twin pronghorn kids and began chasing them. The kids and the coyote ran out of sight at a distance of one-quarter mile, but it appeared that the kids were outdistancing it. The does started to follow but then began grazing.

At 0600, the coyote returned to the area and moved past the bison and pronghorns. One of the does pursued it for a distance of 200 yards until the coyote turned and snapped at her. The doe then returned to the other members of the group. The coyote was not observed again.

In neither of these two instances did the bison appear to be in danger from the coyotes. For that matter, the pronghorns were not threatened except for the pursuit of the kids. On three other occasions, the author observed pronghorn does pursuing single coyotes.

## Bison and man

Roadside signs at Wind Cave caution visitors to remain on the highway near their cars because "buffalo are dangerous." McHugh (1958:8) states that bison are potentially dangerous and should always be approached with caution. He reported six occasions with situations which he believed to be dangerous, and reported being charged at five other times. All of these charges were bluff displays, however. Fuller (1960:17) is of the opinion that bison are neither aggressive nor unpredictable. He reported two potentially dangerous situations, both of which were accidental

encounters.

Bison at Wind Cave generally ignored or moved away from humans except when harassed. On one occasion I approached a bull lying down in a stand of trees. The approach was made to within 20 feet when the bull stood up and made a bluff charge, bouncing on its forelegs 10 feet in my direction. This action was probably precipitated by the fact that the bull was somewhat trapped by the surrounding trees. A hasty retreat by the author did not result in pursuit by the bull.

On November 5, 1969, four large adult bulls were released on the park after being brought from Theodore Roosevelt National Memorial Park. Prior to release, the bulls were held overnight in the corrals. When the animals were to be set free, one of the bulls became very excited when two men attempted to chase it out of the corral. The bull charged one of the men and chased him around an escape tower before the man could scramble up the tower to safety. The bull charged with its eyes open and hooked at the man as he climbed out of reach. The other man in the corral also scooted up an escape tower. The bull then moved back and forth between the towers, pawing and horning the ground, keeping the men "treed." I then drove the study vehicle into the corral in an attempt to rescue the The bull made a bluff charge at the vehicle but did not strike it. men. To prevent damage to the vehicle, retreat seemed most appropriate. The bull followed the retreating vehicle and, once clear of the corral gate, trotted off.

I was never threatened by a cow on the open range. However, one of the undergraduates working at Theodore Roosevelt in 1967 was chased into

a tree by a cow. He later found a calf entrapped in a hole nearby and assumed that the cow was protecting its offspring. McHugh (1958:33) reports 12 attacks against humans by cows with calves but does not describe the situations in detail.

One other incident may be mentioned with respect to bison encounters with man. During one of the immobilizations at which I was not present, a bull apparently moved rapidly in the direction of the observers causing them to climb trees. This type of behavior must be regarded as atypical, however, as the bull was under stress from the drug and handling. It is interesting to note that one of the men became excited and elicited an involuntary micturition response, not unlike the response of bison.

Perhaps the best statement to be made regarding bison and humans is that if humans seek to understand bison behavior and respect the animals as powerful, wild creatures, there is little to fear from these animals. There are certain situations such as a roundup in which dangerous encounters cannot be avoided. The majority of situations, however, are such that observers need not fear the bison as long as a proper distance is maintained. If a visitor moves toward a bison more than one-third the distance from a place of safety, the bison can overtake the person if it decides to charge. As a rule of thumb, this is probably the minimum distance of safety for someone not knowledgeable of the habits of the animal. During the breeding season, approach on foot within 75 yards of a tending bond is potentially dangerous if a place of safety is not close at hand. Few people would wander up to a strange domestic bull. The same precaution should be taken when observing bison. If visitors to areas where bison are present do not place the animals in a position where they "feel threatened" the bison can be observed and enjoyed with little chance for attack.

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#### BISON BEHAVIOR AND THE AMERICAN INDIAN

The first day the Great Spirit planted by the side of the waters the Great Way tree whose boughs extended into the Heavens, by way of which all creatures were sent down upon the Earth, and lastly a Kiowa man and woman who walked about the creation, but in the evening they returned to the Great Way tree, and there they met the buffalo, and the Great Spirit descended and said: "Here are the buffalo. They shall be your food and your raiment, but in the day you shall see them perish from the face of the Earth, then know that the end of the Kiowa is near and the Sun set."

This portion of a Kiowa legend dealing with the creation of man is only one of a great number of such recollections which indicate how important the bison was to the American Indian (Garretson, 1938). Roe (1951) lists the uses which the Indian made of the bison including clothing, bedding, shelter, fuel (droppings), tools, some types of weapons, household utensils, personal and ritualistic adornment, and even symbols of worship. There can be little doubt that there are strong ecological bonds between the bison and the Indians of historic and prehistoric times.

With this type of relationship between man and beast it seems logical to assume that the behavior of the bison was well known to the Indian and thereby affected his way of life. In this section of the dissertation I will comment on this relationship as reflected in the literature and speculate on how a study such as the one at Wind Cave can assist archaeologists and anthropologists in interpreting the bison-Indian associations. This will be accomplished with the use of selected examples and will not be presented as a major synthesis. However, the examples presented will point out the desirability of interdisciplinary efforts in this area.

In discussing the effects of bison behavior on the Indian, one must be careful to avoid attributing all behavior patterns of bison under present conditions to the animals that roamed freely over the plains during historic and prehistoric times. Nevertheless, some speculations must be made as to the similarity of habits of the bison today with earlier ones. Wheat (1972:85) states that archaeologists working with prehistoric kills of bison must assume that the habits of prehistoric and historic bison were essentially the same and that the methods of hunting and utilization by the Indian were similar. While this may be a necessary assumption, it must be made cautiously, especially when considering the size and range of herds today.

The antiquity of the relationship between man and bison is still open to debate. Haynes (1970:17) comments on roving bands of hunters moving down from Alaska 40,000 years ago. There is no archaeological evidence to indicate such an early presence of hunters although species of the genus <u>Bison</u> are known to have existed in North America at that time (5kinner and Kaisen 1947:131). Probably a better estimate of bison as a quarry of man would date to around 8,000 B.C. (Wedel 1961). Works such as those of Kehoe (1967) and Wheat (1972) provide information on the nature of prehistoric bison hunting and use of the animal. Due to the nature of archaeological evidence, however, it is a matter of speculation as to the socio-cultural effects of the bison on these peoples.

Historic evidence of the relationship between bison and Indians reflects the changes in the cultures of the Indian with the advent of a horse culture. The Indians of the Great Plains obtained their first

horses about 1640 from Pueblo Indians who had rebelled against their Spanish masters in New Mexico and ran off to join the tribes in bison country (Haynes, 1970:4). These "runaways" instructed the tribes they joined in the arts of horsemanship. In this manner the horse culture spread throughout the Great Plains in about 120 years. This increased mobility for travel, hunting, and war greatly changed the patterns of the peoples of the plains, including their relationship with the bison.

# Bison Hunting

Wheat (1972:87) points out that the gregarious habits of the bison made the animal a prime candidate for hunting. The possibility of taking large quantities of meat at one time would certainly seem more appealing to a hunting economy than the arduous task of seeking out members of more solitary species. To take advantage of this habit, however, would require varying degrees of nomadism by the hunting groups as well as a fairly well organized division of labor among members of the groups.

Evidence indicates that pre-horse bison hunting which involved mass slaughter was accomplished by two main methods--the surround and the drive (Wheat, 1972:92). The surround generally consisted of setting fire to the prairie grass around the animals or the "human surround" where members of the hunting party circled the bison group and forced them into a small area where they could be killed. The drive consisted of stampeding bison into natural traps such as bogs, driving them into man-made corrals, or driving them over obstacles such as cliffs. Undoubtedly the natural features of the terrain dictated the degree of construction of wing fences

and corrals.

During the study period at Wind Cave, I did not have the opportunity to observe the reaction of bison to fire. However, park personnel indicated that during a major fire in the early 1960's the bison immediately moved out of the vicinity of the flames and none were killed. In the same fire, carcasses of deer and elk were found. Depending on wind and fuel conditions it does not seem unlikely that a fire completely surrounding a group of bison would cause them to remain confined and thereby be killed by hunters on the periphery of the ring. A surround by humans on foot would seem to be more difficult to maintain, however. As indicated earlier, if one animal could break through such a ring, the others would surely follow. While it would seem possible that noise and confusion caused by humans in such a surround could prevent the animals from escaping, the charge of a bison toward a man on foot with primitive weapons would seem difficult if not impossible to stop. As a general observation, the success of this type of surround would seem more likely when used on small groups of young animals. Observations of small groups of yearling bison handled at Custer State Park indicated that these animals might be contained by such a human ring.

The drive style of hunting is dependent upon the ability of the hunter(s) to stampede the bison in the desired direction. Although variations in this hunting technique are documented, all of the methods are somewhat similar to and might be compared with the driving of bison into the corral area at Wind Cave during the annual roundup. The most important difference between today's roundup and the drive methods used by

the Indian is the vastly superior mobility of helicopters and vehicles used in modern-day trapping techniques.

Park personnel have commented that bison at Wind Cave are becoming more difficult to drive into catch pasture and corrals. This is undoubtedly due to the fact that some individual animals have been driven toward the same area year after year. The Indian probably did not encounter this problem to the extent that bison handlers today do because of the high mortality of the animals trapped by the Indians. However, it is reasonable to speculate that the Indian hunters probably had only one opportunity to capture a given group of bison in this manner. If the initial drive failed, the lack of mobility of the hunters coupled with the difficulty of hazing the bison into the proper area a second time might have resulted in failure of the hunt. This is probably the reason for the development of various groups acting as policemen of a hunt to maintain discipline and prevent stampeding the bison too soon (Branch, 1962:39).

Kehoe (1967:68) quotes C. J. Henry of the National Bison Range as saying that the Indian probably attempted to utilize cow herds due to the more desirable meat and the fact that bulls are much more difficult to drive. With respect to the observations made at Wind Cave, there are both pros and cons to this statement. As already indicated, bison cows become more wary of human approach prior to the calving season. This wariness could be used to stampede the animals more easily at that time. However, the ability to approach cow-calf groups during the remainder of the year might allow the hunter to position himself in a more advantageous location

for a drive. The idea that cows would be easier to drive may not be entirely true. As stated earlier, cows were the members of groups that often caused the animals to turn from the trap and break away from the pursuers. With the use of vehicles and helicopters these groups could be overtaken and again turned toward the trap. This would be impossible for men on foot to execute. Kehoe also points out that berries are ripe during the late summer and early fall. As the bison are in prime condition during this time and as the Indian would need to prepare such food items as penmican for the winter, the late summer and early fall might be logical times to drive bison.

Hunting bison on horseback during a prolonged chase is frequently recognized as a method used by Indians for taking the animals. During roundups at Wind Cave and Theodore Roosevelt National Memorial Park I had the opportunity to chase bison on horseback. These chases were not exactly the same as those which must have been used by the Indian as I did not have to get within close range of the animals. Nevertheless, it was obvious that the hunters that took bison in this manner would have to be excellent horsemen with durable and well-trained mounts. During one such chase at Wind Cave, a bison cow was able to outdistance me and escape. In addition, bison turn by pivoting on their front feet which enables the animals to change direction very quickly. In this manner the bison can out-maneuver a horse and rider. This is not likely to happen when a group is being pursued unless the rider approaches quite close to a particular animal and cuts it off from the other members of the group. It is unlikely that anyone who has chased bison on horseback

could fail to develop a deep respect for the bison hunter who dashed in at close quarters to attempt to take a running bison armed only with a bow and arrow or lance.

Wheat (1972:88) indicates that bison have relatively poor eyesight. He bases this conclusion on previous conceptions by other writers. McHugh (1958:6), Fuller (1960:4) and Herrig and Haugen (1970:261) all indicate, however, that bison can see and distinguish between objects at considerable distance. This agrees with observations at Wind Cave where the author was detected by bison over one-half mile away despite downwind approaches. This coupled with the keen senses of smell and hearing indicate that the bison is not the easy quarry that some persons believe. In stalking bull bison at Wind Cave during immobilization activities, it was observed that an approach from the rear with the wind blowing against the observer was possible to within 20 to 30 yards. Any sudden movement was quickly detected by the bison, however, and caused them to turn towards the person stalking them. At this point the bison did not generally take rapid flight unless startled at very close range. However, this response may be due to the fact that the bison at Wind Cave are somewhat used to humans and may not respond in the same manner that earlier free-roaming animals would. The main point to be made is that the bison not only can see objects at great distances but are also capable of detecting sudden movements with a wide peripheral range. This ability surely affected any stalking activities of the bison by the Indian.

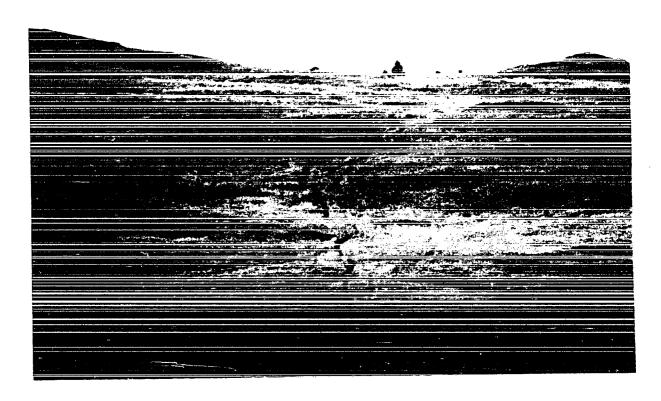
Wheat (1972:87) refers to Dodge's (1882) comments as to the relative

intelligence of the bison. Dodge (1882:291) remarks that the "buffalo is the most stupid of any of the animal creation of which I have knowledge. If it sees or smells no enemy a herd will stand until every individual is shot down." The observations at Wind Cave agree that bison will frequently remain in the vicinity of a wounded member and will mill around in an excited manner. However, this trait is not a measure of "intelligence" but rather a behavior pattern associated with gregarious tendencies. Also, I do not know whether or not the animals would respond in this manner to an "enemy" at close range such as would be required for primitive weapons as compared to firearms. In contrast to Dodge's statement, Brown (1953:72) quotes Black Elk of the Oglala Sloux as saying that "the buffalo is wise in many things and, thus we should learn from him and should always be as a relative with him." These words are from a representative of a people who lived in close association with the bison for many years. The relative measures of intelligence would seem then to be reflections of the feelings of the observer and not appropriate evaluations of the animal itself.

# **Bison Trails**

As indicated earlier, bison travel in two manners--spread out, especially while grazing, and in a single file or column fashion when moving to and from water or into different areas of the park. The latter type of movement may cause the formations of trails across the prairie which are furrows one to two feet wide denuded of vegetation (Fig. 52). Garretson (1938:55-6) indicates that trails were formed in this manner

Fig. 52. Bison trails. These trails are caused by bison moving single file or column fashion. The trails consist of furrows one or two feet wide which have been denuded of vegetation by the bison travel



during earlier times and that these trails were quite common on the prairies. Wheat (1972:91) indicates that an arroyo at the Olsen-Chubbuck site had its origins in the erosion of one such trail.

The significance of these trails to the Indian can only be guessed. As a general observation, however, I found that traveling on foot or horseback at Wind Cave was far easier when the trails were followed than when striking out in a straight line. This was particularly evident in the effect on the stamina of a horse carrying a rider. Any experienced woodsman knows that travel in rugged terrain is made easier by taking advantage of existing game trails. It seems reasonable that the Indian also recognized this and took advantage of the bison trails in traveling over the prairie. This might especially be expected of Indian groups before the horse became available..

Bison trails at Wind Cave appeared to be random in placement. Some trails did lead to watering sites on the area. If Garretson (1938) and other authors are correct in stating that these trails frequently led to water in the early days, the Indian might easily have taken advantage of this in locating and traveling to water supplies. Depending on the frequency of use of individual trails by bison, these paths could be used to locate game and provide sites of ambush. The fact that the bison at Wind Cave are confined to the area makes this issue a questionable one.

# Bison Behavior and Indian Religion

There can be little doubt that the relationship between the Indian and the bison carried over into the realm of religion. I will not attempt

to document all of the legends and ceremonies of the American Indian which included reference to bison. Several examples of this relationship may be drawn from Brown (1953) in his recordings of Black Elk's account of the Seven Rites of the Oglala Sioux.

The bison was the most important four-legged animal to the Sioux, for it supplied food, clothing, and even homes. Because the bison "contained all things within himself," it was the symbol of the universe. Everything is symbolically contained within this animal---the earth and all that grows, all animals, and even people. Each specific part of the bison represents a part of creation for the Sioux. The four legs of the bison represent the four ages which are an integral condition of creation. Certain meat from the shoulder of the animal represents mankind and, according to Brown, is regarded by the Sioux in much the same way as is the holy Eucharist by the Christian. The belief in the wisdom of the bison by the Sioux has already been mentioned.

The skull of the bison is an integral part of the Sun Dance, chief religious festival of the Sioux. As part of this ceremony, grass, tobacco, a robe, paint, and water are symbolically "given" to the bison by the Sioux people as the chief of all four-legged animals. The Sioux believe that the bison showed them the rite of purification of the young. This is referred to as the bison purifying "their children and preparing them for bearing fruit." While this reference is not clear, it may have some relationship to the grooming characteristics of bison cows for

calves.

Another ceremony of the Sioux in which the bison is important deals with preparing a girl for womanhood. In this ceremony, the leader is believed to receive the power of the bison. A round circle is scraped on the ground to represent a bison wallow. One of the leaders bellows like a bison and blows red dust out of the mouth "just as a buffalo cow is able to do when she has a calf." The author does not understand the significance of this last reference to dust. Could it refer to dust blown from the ground by a cow during the process of parturition? During the entire ceremony, the participants are referred to by such names as Slow Buffalo and White Buffalo Cow Woman.

These are just a few examples of reference to bison in Sioux religion. Certainly there are many more references to the bison in the religious activities of other tribes. It would seem advantageous to a student of these ceremonies and beliefs to obtain a working knowledge of the behavior of the bison to better understand the beliefs of the Indian.

# Conclusions

This section represents a minute sampling of how the behavior of the bison may be used in interpreting the behavior and activities of the Indians who depended on this species for sustenance. It does point out how an interdisciplinary approach to the problems of understanding the relationships between the bison and the Indian can be desirable and profitable. Further work in this area is certainly recommended.

#### SUMMARY

This study was carried out with three main goals. The first goal
was to add to the increasing knowledge of the natural history of the
bison. Secondly, it was believed that this study and others like it may
be of particular use to antropologists studying the American Indian,
especially the tribes of the Great Plains. The third goal was to provide
information which will increase the recreation potential of the bison.
 Field work was carried out from June 1 to November 17, 1968 and
March 10, 1969 to February 24, 1970. The study area was Wind Cave
National Park in southwest South Dakota. The park represents an ecotone
between the coniferous forest of the Black Hills and the grasslands of
South Dakota. The bison herd was maintained between approximately 225
and 300 animals during the study.

3. A total of 3,363 observations of bison were made during a total of 2,929 field hours.

4. Bison were observed in two main types of groups throughout the year. These groups were classified as cow-calf groups and bull groups. In addition, bulls ranging alone were designated as lone bulls. Cow-calf groups included adult cows, calves, yearlings of both sexes, and bulls up to 3 years of age. They also included mature bulls during the rut. 5. Bull groups varied in size from 2 to 17 animals and consisted of bulls 4 years old and older. Lone bulls accounted for 525 (58,6%) of 896 observations of bull groupings.

6. Lone bulls and bull groups were observed in all parts of the park but were concentrated in the southwest portion. During the rut these

bulls moved into the areas of the cow-calf groups and joined them.
7. Group integrity in bull groups was not as well defined as in cow-calf groups. The longest recorded period of association was 9 days in October of 1969 when two individuals remained together. Leadership and allelomimetic (contagious) behavior in bull groups was variable.
8. Bull groups generally moved from one area to another by traveling in a single file. Distances between members varied from 10 yards up to one-quarter mile and were dependent on time delays for members of a group to imitate the behavior of another member wandering off.

9. Lone bulls and bull groups were much less wary of human approach than cow-calf groups. Flight distance for bulls was usually under 100 vards.

10. Habitat preference for lone bulls and bull groups indicated greatest use of grasslands. However, there was seasonal selection for woodlands and prairie dog towns during the spring and summer months.
11. Cow-calf groups varied in size from 3 to 240 animals. These groups were more complex in their structure than bull groups.
12. Cow-calf groups frequented areas in the northern and eastern parts of the park more than lone bulls and bull groups. Some movements into the southwestern part of the park were attributed to disturbances by man.

13. "Solidarity" of activity was much more common in cow-calf groups than in bull groups. Leadership in these groups was by a cow, usually a cow with a calf. Grazing and moving to different locations in these groups were usually stimulated by a cow. Observations during the

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roundup added support to this hypothesis.

14. Flight distances in cow-calf groups showed seasonal variation. During the calving season (April through June) cow-calf groups were quite wary of human approach. During a short period following the annual roundup these groups were again wary of approach. During the other seasons of the year these groups could be approached with relative ease. 15. Vocalizations by cows and calves were grunting sounds. Cows calling calves grunted in a series at a frequency of one grunt per second. The grunts of calves could be distinguished from those of cows by their higher pitch.

16. Bulls older than 5 years were never heard to make a grunting sound. These bulls gave snorts which sounded like puffing sounds made by quick contractions of the abdominal muscles to force air through the nostrils. These snorts were commonly given by adult bulls entering or moving through cow-calf groups, particularly prior to and during the rut. 17. During the rut the bulls roar. This roar is associated with high levels of excitement. The duration of roars varied from 1 to 5 seconds.

18. Wallowing is the most conspicuous form of grooming in the bison. Bison commonly wallow in areas where the vegetation has been denuded such as in prairie dog towns. Traditional wallowing sites which the bison have created by horning and pawing the sod and which are maintained through continual use were observed over the entire park. 19. Adult bull bison wallowed more frequently than cows, calves, and juveniles. As evidence of this, these bulls lose the shed winter hair as

early as June while cows usually retained this hair in large patches throughout the summer and early fall. Wallowing is used as a displacement activity by bulls during agonistic encounters in the rut.

20. Rubbing on the ground and objects such as trees, rocks and signs was also a common grooming practice in bison. Trees frequently used in this activity had patches of bark rubbed off.

21. Bison licked all parts of their bodies with the exceptions of the under part of the chin and neck, the chest region, the head from above the nose back, the center of the back, and the perianal region. Rear hooves were used to scratch the head and neck regions and around the eyes. Horns were used by cows and young bulls (before the tips were broken and worn) to scratch the hump region.

22. Mutual grooming was common among juveniles and between cows and their calves. During the first two weeks of the calf's life the cow frequently licks it over the entire body including the perianal region and the umbilicus.

23. Tail switching is a part of grooming behavior in the bison in that it was commonly used to brush flies and other irritants from the surface of the skin on the rump and hip area.

24. Bison groups generally grazed actively during five periods of the day--just at dawn, just before midday, in the middle of the afternoon, one or two hours before sunset, and frequently around midnight. Grazing periods for bull groups and lone bulls followed this general trend but were more variable than in cow-calf groups.

25. Bison grazed in a "wave" fashion, with members spread out laterally

behind the leader(s). Grazing movements varied from one-quarter mile to 3 miles. Times of concentrated grazing varied from 1 to 3 hours. Group movements not associated with grazing were distinguished from grazing movements in that the former consisted of the animals moving in a column form or single file. The longest such movement recorded was 7 miles.

26. During the summers, cow-calf groups visited watering areas at least once a day. During periods when bison groups remained in the vicinity of a pond, the animals moved to and from the water in a single file. Bison characteristically waded into the water before drinking, even the calves. Both bulls and cows almost invariably urinated into the water upon wading into it.

27. During the winter months bison were observed eating snow. When ice covered small puddles, bison at times broke through with their noses and front hooves. Holes made in this manner were observed being used by pronghorns and elk.

28. Bison visited salt blocks placed at particular locations on the area but not on a regular basis. They also licked and ate the soil in the vicinity of blocks or where blocks were known to have existed previously.
29. Bison deposit their excreta haphazardly with respect to location.
A special stance is assumed for defecation. Defecation was also an indicator of excitement in bison.

30. Female bison assumed a position much like that of defecation for urination. The urine was voided with some degree of force resulting in an arc of fluid extending 2 to 3 feet behind the animals.

31. Bull bison urinated with the tail slightly elevated as in defecation but generally did not arch the back. Urine was passed slowly by bulls and with not nearly as much pressure as in cows. During the rut bulls sometimes urinated while having a partial erection. This resulted in a forced squirting of urine which may have been a "self-marking" mechanism. 32. Bull bison frequently urinated while wallowing, particularly during the rut. This may be related to changes in hormone levels, particularly testosterone.

33. Only 10 observations of violent combat in mature bulls were made during the study. Most of these encounters lasted less than 1 minute with the longest lasting 1 minute and 45 seconds. There was one atypical encounter which lasted a total of 17 minutes, but this did not entail continuous fighting.

34. Bulls observed engaging in vicious combat approached to within 4 feet of each other while roaring continuously. They then lunged at each other, striking head on and hooking with their horns. The power thrust appeared to be delivered with the hind legs. Such encounters caused an increase in group excitement.

35. Bluff displays varied from direct looks to charges which stopped short of combat. These charges entailed an animal jumping towards another with the front legs held stiff so that the animal bounced for a few steps.

36. Agonistic behavior in cows included all of the displays but did not include violent combat. Both bulls and cows used their hind hooves for kicking under certain conditions.

37. Except in the mildest forms, the raising of the tail was the best indicator of excitement in bison. Higher tail positions indicated greater levels of excitement.

38. Due to the size of the area and large number of animals involved, a well defined dominance hierarchy could not be identified. However, evidence of this type of order was noted as described in previous studies. 39. Three cases of adult bull mortality were recorded which were attributed to agonistic encounters. One other bull was destroyed due to serious wounds received in such an encounter. One incident of calf mortality was recorded which may have been the result of agonistic behavior.

40. Using 2 years as the minimum breeding age for cows with no maximum, 78 cows were of calf-bearing age in 1969. A total of 62 calves were observed on the area that year. This indicated a minimum calving rate of 79.5%.

41. Combined male:female sex ratios for 1968 and 1969 was 50:50 exactly based on 124 calves. In 1968 the ratio was 57.1:42.9 as compared to 42.6:57.4 in 1969.

42. The first calves were observed on the area on April 21 in 1969. By May 13, a total of 40 calves was observed representing 64.5% of the years production. This 23 day period represented the peak of the calving season.

43. Pregnant cows were identified by **distention** of the abdomen primarily as this indicator was found to be most suitable under field conditions.

44. Increased wariness of cows during the calving seasons made observations of parturient behavior difficult. Despite a total of 768 field hours during the calving seasons, only one birth was witnessed. This occurred on the periphery of a cow-calf group. The newborn calf was able to stand within 40 minutes of birth and began suckling within 48 minutes. During the first few hours of the calf's life the cow spent a great deal of time licking the calf.

45. Calves used a parallel suckling posture from the time of birth. They also attempted to suckle from behind when cows were walking. Calves "headed off" cows to make them stand for nursing.

46. Bison calves were observed engaged in grazing behavior during the second week of life. Suckling was observed throughout the year with 21 instances of yearlings attempting to suckle as well as one 2-year old bull. Suckling activity decreased during the fall and winter months. The weaning of the calves may have been initiated during the rut and probably is related to increasing size of the calf and increased vigor of bunting of the cow during suckling.

47. Bison calves remained very close to the mother cows during the first week of life. Calves usually oriented themselves so that they were facing the cows.

48. Calves roamed farther from their mothers during the third week of life and formed calf play groups at this time. These groups were loosely organized.

49. Calves returned to the mother cows when approached or threatened and invariably began suckling.

50. Bison calves spent a great deal of time lying down during the first month of life. They assumed a variety of postures for doing this. Calves were observed to lie on their sides for much longer periods than adults. 51. Play activities in bison calves included chasing each other, mock battles, mounting behavior. Calves also frolicked by themselves. 52. Bulls mature sexually by the time they are 3-years old. However, courtship and presumably breeding activity was restricted to full grown bulls.

53. The lip curl posture in bison was observed in all ages and both sexes but increased in frequency in bulls during the rut. This is an indication that olfaction is fundamental in the stimulation of reproductive processes. These lip curls were generally associated with investigating urine and/or the vulvas of cows.

54. Sexual investigatory behavior of bulls included sniffing and licking the vulva regions of cows, generally followed by lip curls. This genital stimulation may affect oestrus in the female. The first investigation by an adult bull in a cow-calf group was observed on June 21 in 1968. This investigatory behavior increased when lone bulls and bull groups joined the cow-calf groups during that season.

55. Bison bulls are promiscuous while cows are presumably served by only one bull. The courtship bond between the bull and the cow is termed the tending bond and is characterized by the bull attempting to isolate the cow from other members of the group. Duration of these bonds was variable. During these bonds bulls demonstrated intolerance of other group members of either sex, but particularly of other adult bulls.

56. Tending bonds early in the rutting season involved primarily younger cows and cows without calves.

57. Despite 1,572 hours in the field during June-September of 1968 and 1969, no complete copulation was observed. False mounts were recorded. Chin-resting or a head throw usually preceded these attempted mountings. 58. Chases occurred during July and August of both years. These chases may serve as a dispersal mechanism prior to actual copulation to diminish combat encounters.

59. One observation was made of possible masturbation.

60. Bison harassed elk calves on two occasions and a mature bull elk on another. Both the calves and the bull elk apparently survived these encounters.

61. No predators at Wind Cave were known to take bison.

62. Potentially dangerous situations for human encounters with bison were recorded and involved some form of harassment or threat of the bison by the humans.

63. Interdisciplinary efforts between anthropologists and persons working with bison behavior are recommended.

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## APPENDIX

Appendix Table 1. Distribution of observations and field hours at Wind Cave National Park with numbers and mean sizes of groups observed

				Mean sizes		
		Total		of	Lone bulls	Mean sizes
	Hours	obser-	Cow-calf	cow-calf	and bull	of
Month	afield	vations	groups	groups	groups	bull groups
·			A	QA		
			1968			
<b>.</b>	0.7.6	0.7.0		<i></i>		
June 18	216	310	23	68.8	65	3.3
July	222	396	20	144.5	56	1.6
Aug.	228	283	26	54.4	57	1.0
Sept.	103	75	12	96.9	32	1.5
Oct.	150	79	7	40.7	33	2.4
Total	<u>91</u> 9	1143	88		243	
			<u> 1969–70</u>	<u>)</u>		
Mar.	140	150	24	41.1	57	3.4
Apr.	173	295	43	31.9	112	3.5
May	189	206	17	57.0	88	2.8
June	190	200	22	78.9	84	2.5
July	228	403	49	66.9	100	1.4
Aug.	200	266	24	76.2	68	1.2
Sept.	185	241	20	93.5	46	1.5
Oct.	177	113	11	38.3	33	2.9
Nov.	140	62	8	55.8	18	2.1
Dec.	116	83	14	39.7	13	3.3
Jan.	137	107	16	77.1	19	3.3
Feb.	135	94	10	72.4	15	4.8
Total	2010	2220	258		653	
Grand total	. 2929	3363	346		896	

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Month	Grazing	Watering	Moving	Loafing
		1968		
Terre	00		0	
June	80	15	8	44 75
July	63 	22	17	75 53
Áug.	35 no	25	19	
Sept.	22	14	2 3	45 37
Oct.	35	2	3	37
Total	265	78	49	254
		1969-70		
Mar.	53	1	9	48
Apr.	110	5	20	67
May	80	16	8	48
June	72	21	15	75
July	91	25	31	109
Aug.	59	27	<u>1</u> 4	56
Sept.	36	14	11	55
Oct.	55	13	8	48
Nov.	32	1	17	47
Dec.	36	2	2	32
Jan.	50	0	6	43
Feb.	56	0	2	36
Total	790	125	143	664
Grand total	1055	203	192	918

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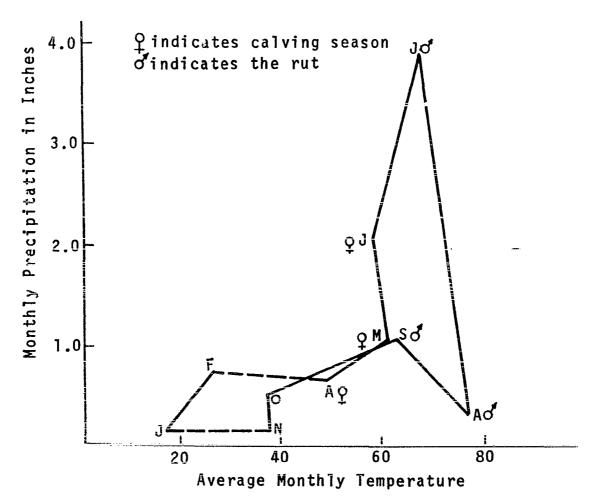
## Appendix Table 2. Daily round activity observations of bison at Wind Cave National Park

Month	Open grassland	Prairie dog towns	Woodlands
		1968	
June	56	3	11
July	31	4	15
Aug.	30	10	16
Sept.	23	0	12
Oct.	34	0	1
Total	174	17	55
	_	1969-70	
Mar.	56	3	6
Apr.	100	8	11
May	58	19	25
June	77	7	15
July	79	13	17
Aug.	38	8	19
Sept.	29	8	13
Oct.	37	17	5
Nov.	18	1	5 5 5 8
Dec.	ŹŻ	1	5
Jan.	21	0	
Feb.	24	1	4
Total	559	86	131
Grand total	733	103	186

Appendix Table 3. Observations of lone bulls and bull groups by habitat types at Wind Cave National Park

Month	Open grassland	Prairie dog towns	Woodlands
		1968	
-			_
June	45	16	5
July	62	38	4
Aug.	52	31	1
Sept.	30	1	3
Oct.	31	6	5
Total	220	92	18
	_	1969-70	
Mar.	42	0	1
Apr.	66	13	3
May	58	19	25
June	42	18	4
July	79	13	17
Aug.	55	12	4
Sept.	42	0	5
Ũct.	40	<u>4</u>	11
Nov.	29	1	2
Dec.	35	7	2 2 8
Jan.	59	3	
Feb.	56	6	3
Total	603	104	86
Grand total	823	196	104

Appendix Table 4. Observations of cow-calf groups by habitat types at Wind Cave National Park



Appendix Fig. 1. Climograph with monthly precipitation and average monthly temperatures for 1969 at Wind Cave National Park. Totals not available for March and December