Life History and Ecology

Behavior

The size of a bison herd is heavily dependent on sex and age structure and on habitat and forage availability (Berger and Cunningham, 1994a). Early reports of travelers exploring the American West described immense herds of bison that stretched across river valleys and darkened the plains. These reports helped to fuel inflated population estimates and reinforced the idea that bison were an inexhaustible resource. The size of these historic herds were influenced by a number of factors including variation in forage quantity and quality, environmental influences, and pressure from human activity (Bamforth, 1987). The early reports of vast herds did not take into account the fact that bison tend to congregate in larger herds mainly during the summer breeding season, and only in favorable feeding habitat (Nowak and Paradiso, 1983; Bamforth, 1987; Berger and Cunningham, 1994a; Aune et al., 1998; Isenberg, 2000). Historically bison tended to divide into smaller herds during the winter as "the need to scatter was also dictated by the poor quality and reduced quantity of forage at this time of year, which could not sustain large groups of animals" (Brink, 2008, pp. 64).

Though bison will congregate into larger aggregates during the summer months, throughout the remainder of the year cows, calves, and immature males tend to form smaller "cow" groups with an average of 10 to 20 bison, though numbers can reach upward of 50 to 70 bison as smaller groups converge (McHugh, 1972; Nowak and Paradiso, 1983; Isenberg, 2000; Long, 2003; Picton, 2005; FWP and MNHP, 2010a). During a study of bison in northern Yellowstone National Park, Aune et al. (1998) observed that mean group size for cow groups was 27 in the winter and 32 in the spring. They also observed that females with calves may form "nursery groups" during the calving season, which may reach 100 to 200 animals (Aune et al., 1998).

Larger cow groups will separate into smaller groups of 10 to 20 in order to feed (Picton, 2005). During his study of bison in Utah, Van Vuren (1980) observed that cow groups expressed a high degree of fluidity, with groups tending to remain together for a few days before dividing and combining with another group. The degree of fluidity was contingent on proximity to other bison groups (Van Vuren, 1980). Aune et al. (1998) also noted that group fidelity appears to be temporal and that there appears to be a very fluid and dynamic social structure within cow groups. Older females tend to be more dominant within these smaller cow groups (Rutberg, 1986; Foresman, 2001).

Solitary bull. PHOTO CREDIT: S. ADAMS

The bulls tend to remain solitary or form small groups of up to five bulls during most of the year, joining with the cow groups only during the breeding season (McHugh, 1972; Long, 2003; Reynolds et al., 2003). During observations of bison in Badlands National Park, Berger and Cunningham (1994a) found that even during more social months the mean bull group size was less than three, with one being the median throughout the year (pp. 75). Bull groups tend to consist of males over the age of four (McHugh, 1972).

The type of habitat that a herd occupies can also have an effect on its size. Group sizes tend to be smaller in mountainous or mixed terrain than in open prairie (McHugh, 1972; Gates et al., 2010). Berger and Cunningham (1994a) found that habitat seemed to have a greater effect on the size of cow groups than bull groups. They found that there was a 50 percent reduction in the size of a herd from prairie habitat to habitat consisting of ravines and rolling hills.

Bison are also known to congregate in larger groups around permanent sources of water, but then will separate to feed (Bamforth, 1987). Bison density averages from one to four per square mile depending on the range conditions (Long, 2003). Based on his observations of the bison herd that once freely roamed on the Flathead Indian Reservation, Andrew Stinger recalled that "contrary to a current idea, our buffalo in the Flathead Valley did not roam in one large herd; and I presume that was because there were no mass migrations during summer and winter, as had been the habit of the Plains bison. Here, a leader bull, and possibly a younger aspirant to that station, would head a band, composed of some 20 or 25 cows and calves" (Whealdon, 2001, pp. 62).

Activity of both Native Americans and Europeans is believed to have influenced the size of historic bison herds and their movements. The amplification of hunting pressure increased the overall mobility of the prey, and as individual bison fled it would have caused the entire herd and possibly surrounding herds to flee as well (Bamforth, 1987). Prior to the introduction of horses, Native Americans tended to slaughter entire small herds. Native American hunters believed that small herds must be slaughtered entirely or the surviving bison would flee and warn other herds, making them more difficult to hunt (Krech III, 1999; Picton, 2005; Brink, 2008). The reasoning behind this practice was supported by the observations of early European Americans that once a bison herd had experienced human predation, it would flee at the slightest sign or smell of man (Picton, 2005). Bison have a highly developed sense of smell, which is their primary defense mechanism, and "perhaps because they are not very keen of sight, bison are remarkably sensitive to any unusual movement in their environment" (Brink, 2008, pp. 100).

The use of horses caused bison herds to become more mobile and did not allow for the slaughter of whole herds as occurred with the use of a buffalo jump or pound. The removal of random individuals from a herd led to more frequent stampedes, as well as larger aggregations of animals in the vicinity of the hunting area (Bamforth, 1987). Human settlement and expansion into an area often prevented the bison from utilizing major water sources, trails, and resources, thus leading to an increase in bison in the neighboring region (Bamforth, 1987). It is speculated that the settlement of the east caused the bison to migrate into the western regions, thus increasing the density of the animals within the region and triggering increased herd size and mobility (Bamforth, 1987).

The home range of free-ranging bison varies with habitat productivity (Reynolds et al., 2003). The average home range of a bison herd extends from 18 to 62 square miles depending on the season and the quality of forage (Nowak and Paradiso, 1983; Long, 2003). Aune et al. (1998) observed that the average home range for female bison in northern Yellowstone National Park was approximately 208 square miles. Herds utilize smaller home ranges during the summer months and larger ranges during the winter (Foresman, 2001). Aune et al. (1998) found that home ranges within northern Yellowstone appear to become larger during severe winters due to the long-range movements bison undertake to reach winter habitats along the northern border of the park. When in habitat of lower productivity, bison will increase the size of their home range (Foresman, 2001).

As grassland ungulates, bison must modify their behavior to withstand wide spatial variations in resource quality and availability (Guthrie, 1980). "Temporal and spatial variations in range use are likely related to such factors as tradition, forage availability and nutritional quality, macroclimatic and microclimatic variations, open water, shelter, and insect harassment" (Reynolds et al., 2003, pp. 1023). Bison may have to travel extensive distances daily to find water, search for areas of recent precipitation, and follow phenological peaks in plant growth (Guthrie, 1980). "The patchy distribution of bison was a fact commented on by European travelers. Josiah Gregg recorded that "as they incline to migrate en masse from place to place, it sometimes happens, that, for several days' travel together, not a single one is to be met with; but, in other places, many thousands are often seen at one view." Edwin James camped on the Platte River with the plains around him covered with "immense herds of bison, grazing in undisturbed possession and obscuring, with the density of their numbers, the verdant plain." Surveying the same territory the next morning, he remarked with astonishment that "upon all the plain which last evening was so teeming with noble animals, not one remained."(Brink, 2008, pp. 229).

Within their home range, bison tend to move around 1.8 miles daily (Nowak and Paradiso, 1983; Long, 2003). Bison move frequently within their home ranges, and Van Vuren (1980; 1983) noted that herds within the Henry Mountains seldom remained in one place for more then three days. Migration is closely associated with locations of permanent water and forage quantity and quality due to seasonal changes and precipitation patterns (Bamforth, 1987). Historically bison herds may have migrated a few hundred miles south in search of higher-quality winter habitat (Nowak and Paradiso, 1983; Long, 2003). During her study of bison in Yellowstone National Park, Meagher (1973) observed that during the spring bison moved from lower wintering valleys to higher summer ranges, and would then reverse this altitudinal migration in the fall. Van Vuren (1980) observed in Utah that during the summer, bison followed a pattern of using the northern part of the range in early summer, with a gradual southward shift as the summer progressed.

Historically a large number of bison wintered on the northern plains, "just not on the flat and exposed windswept prairies" (Brink, 2008, pp. 62). "As the air turned crisp and ice began to form on the edges of ponds and streams, their instinct told them that it was time to head for sheltered areas . . . These areas weren't necessarily any warmer or less snow-covered, but they all had one thing in common—they provided refuge from the wind.

Typical winter sheltering spots for bison included deep valleys of rivers, creeks, and coulees, thick groves of trees and brush, and hilly or broken county where there are options to move out of the wind" (Brink, 2008, pp. 62–63). During the winter in Yellowstone National Park, bison spend the majority of their time locating and consuming forage, and spend almost one-third of this time displacing snow in order to reach the underlying vegetation (Bruggeman, 2006; Bruggeman et al., 2009; White et al., 2011b). "Thus, snow is the primary factor that reduces foraging efficiency and bison prefer patches with minimal snowpack compared to the surrounding landscape" (Bruggeman, 2006; White et al., 2011b, pp. 11). Bison would begin to move back out onto the plains as winter transitioned to spring. "By March the grip of winter loosened and the Plains once again became a tolerant friend. Herds moved out of sheltered valleys and hilly country but stayed close enough to move back in case of all-too-common late winter storms" (Brink, 2008, pp. 64).

Bison engage in a wallowing behavior that provides evidence of their movements on the landscape even after they are physically absent from an area. During his stay at Montana's Fort Union in 1843, John J. Audubon observed that "the buffalos, old and young, are fond of rolling on the ground in the manner of horses, and turn quite over; this is done not only to clean themselves, but to also rub off the loose old coats of hair and wool that hangs about their body like so many large, dirty rags" (Audubon, 1900, pp. 36). There are reports of soil depressions visible on the landscape today that have been attributed to relic bison wallows. Coppedge et al. (1999) examined soil depressions on The Nature Conservancy's Tallgrass Prairie Preserve to determine if they were actually bison wallows or if they were from geological processes. Their examination found that "these soil depressions, and possibly other 'relict' bison wallows, are not persistent soil disturbances resulting from bison wallowing, but small patches of landscape and soil heterogeneity resulting from variation in underlying geological materials" (pp. 382). The lifespan of bison wallows has not yet been established, nor has the role that different soil types play in the persistence of wallows (Coppedge, et al., 1999).

Cow bison wallowing. PHOTO CREDIT: J PEACO; COURTESY NPS

Bison of all ages and sex classes roll in soft dirt while scraping their horns and hooves against the ground (McMillan et al., 2000; Reynolds et al., 2003; Gates et al., 2010). This behavior forms a circular to oval-shaped bare soil depression (Coppedge et al., 1999). Meagher (1973) observed that bison tend to utilize the same wallows annually. Wallowing is associated with the relief of insect and parasite irritation, shedding, and potentially as a means of thermoregulation, as bison can lower their body temperature through contact with cooler soil (Nowak and Paradiso, 1983; McMillan et al., 2000; Lott, 2002; Reynolds et al., 2003; Picton, 2005). Wallowing is also associated with reproduction. Bulls will urinate in a wallow and then both the bull and cows will roll in the urine. The pheromones in the urine induce the cows to come into estrus, helping to coordinate the estrus cycle of the females within the herd (Bowyer et al., 1998; Picton, 2005). The urine may also advertise a bull's fitness level to other competing bulls (Bowyer et al., 1998; Lott, 2002).

Bison wallows increase the heterogeneity of the landscape. The soil within a wallow becomes exposed and compacted. This compacted shallow bowl collects rainwater and creates a microenvironment in which seeds can sprout. The seedlings of sedges and rushes that are otherwise absent in the prairie occur in wallows (Coppedge et al., 1999; Knapp et al., 1999; Lott, 2002).

Roughly 3,000 head of bison are managed with minimal contact on approximately 113,000 acres within Turner Enterprises Inc.'s Flying D Ranch, located in southwest Montana. Though there are some concentrated wallows, there are not a large number of wallows across the landscape and negative impacts from wallowing have not been observed. The wallows are approximately eight to 10 feet in diameter and tend to occur on flatter ground consisting of finer texture soils. Ranch management notes that wallows have been a minimal issue (Turner Enterprises Inc., personal communication).

Bison of all age and sex classes also engage in a behavior referred to as horning, which involves the rubbing of an object with the head, horns, neck, or shoulders (McHugh, 1958; Coppedge and Shaw, 1997). Horning is believed to be associated with relief from insect irritation, though it may also be a behavioral display or associated with coat shedding (McHugh 1958; Coppedge and Shaw, 1997; Gates et al., 2010). Horning typically involves rubbing on a shrub or small tree, though bison may utilize man-made objects as well (Gates et al., 2010). Bison prefer to horn aromatic shrubs, saplings, and treated utility poles, which may contain insecticidal or insect-deterring properties, to gain relief from insects (Coppedge and Shaw, 1997). Bowyer et al. (1998) hypothesized that female bison may rub trees to advertise estrus. They observed that females rub trees more often than males, which they felt indicated the behavior was related to the reproductive status of a female during the rut. Robert Vaughen, one of the first pioneers in Montana, observed near the Sun River that "in the grove some of these monarchs were rubbing against the trees, and, I should judge, were enjoying themselves immensely" (Vaughn, 1900, pp. 77).

Habitat

Bison evolved through natural selection as a "dominant grazer" on complex landscapes (Fuhlendorf et al., 2010), and historically occupied a variety of habitats. Bison were found throughout the prairies, arid plains and grasslands, meadows, river valleys, aspen parklands, coniferous forests, woodlands, and openings in boreal forests (Long, 2003; Burde and Feldhamer, 2005; FWP and MNHP, 2010a).

PHOTO CREDIT: GYC

Bison utilize the woodlands in the summer for shade, and in the winter when the accumulation of snow prevents feeding in more open terrain (Meagher, 1978; Burde and Feldhamer, 2005). Berger and Cunningham (1994a) observed that bulls are more common in breaks, woody draws, and ravines than females. The cow groups are more common on prairie habitat. Currently most managed bison preserves confine bison to small reserves of land that are often outside of the short-grass plains, which was one of their main historic habitats (Isenberg, 2000). Within the National Bison Range in Montana, the bison occupy Palouse prairie and montane forest (FWP and MNHP, 2010a).

Foraging Ecology and Diet Composition

Within this section the diet and foraging ecology of bison is often compared with domestic cattle. It is important to keep in mind that bison have mainly evolved through natural selection on complex landscapes, whereas cattle have been artificially selected for agricultural production and human use for thousands of years (Fuhlendorf et al., 2010). Therefore, Fuhlendorf et al. (2010) note that while "it is a reasonable prediction that when these species are managed as wild populations on complex landscapes, there could certainly be differences in how they handle threats and limited resources. It is less reasonable to predict differences in ecological effects when both species are compared within an agricultural setting" (pp. 5). It is also important to keep in mind that the term "cattle" represents a wide variety of cattle species that have different abilities to adapt to the landscape and have differing ecological needs (Fuhlendorf et al., 2010). The differences and similarities of bison and cattle on complex landscapes have not been adequately studied, and there are few studies that directly compare bison and cattle (Fuhlendorf et al., 2010). Many of the studies in this section compare the two species within agricultural settings, not in direct comparison, or in limited environments, and while these studies help to draw a general hypothesis, there needs to be further testing with stricter experimental controls.


PHOTO CREDIT: FWP

Bison are a diurnal and crepuscular species, meaning that they are mostly active during the day and at twilight (Nowak and Paradiso, 1983; Long, 2003; Reynolds et al., 2003). Though depending on the season and the quality of forage, bison have been observed to be active on moonlit nights (Long, 2003; Reynolds et al., 2003).

Bison are ruminants with a four-chambered stomach system that allows them to effectively digest plant material. Bison have a mutually beneficial, or symbiotic, relationship with microorganisms including bacteria and protozoa, which allow an increased utilization of plant material than would occur in the microorganisms' absence (Feist, 1999; Picton, 2005; Gates et al., 2010). Bison typically forage between 9 to 11 hours daily, but will increase their foraging if the quality of food is low (Picton, 2005). Bison alternate between active foraging and passive ruminating to allow time for the microorganisms to break down the plant material (Foresman, 2001). The large size of the bison allows for a larger digestion vat, thereby allowing bison to utilize lower-quality forage than other ungulates, such as elk, cattle, or deer. This ability to utilize lower-quality forage is one of the reasons why when bison occur on North American grasslands they can be major influent animals.

Reynolds et al. (2003) note that "much of what is known about bison digestion and nutrition has been extrapolated from beef cattle requirements and digestive physiology," and that "specific energy, protein, mineral, and vitamin requirements have not been developed for bison" (pp. 1019). Within an agricultural setting, on average the total digestive tract retention time for bison is 78.8 hours, compared to 68.7 hours for cattle (Feist, 1999). This increase in digestion time allows bison to digest 64 percent of sedge hay and 74 percent of grass hay, compared to cattle, which digest 58 percent of sedge hay and 62 percent of grass hay (Feist, 1999). In a study comparing the diet compositions of bison and cattle on short-grass plains, Peden et al. (1974) found that "bison appear to have a greater digestive power than cattle when consuming low protein, poor quality forage . . ." (pp. 497). Plumb and Dodd (1993), however, found in a comparison of bison and cattle grazing on mixed prairie that their results "do not completely support the hypothesis that bison have the ability to digest lower quality forages better than cattle" (pp. 63). Bison and cattle were managed within enclosed pastures in both studies.

In a study that compared the foraging behavior of bison and cattle in Utah, Van Vuren (2001) observed that bison and cattle differ in the elevation and degree of slope in which they graze, with bison more often grazing at higher elevations. Topography and the degree of slope are contributing factors in the grazing pattern of cattle. Cattle will not generally graze on slopes with a grade exceeding 4 degrees while bison have been observed grazing on slopes up to 32 degrees (Van Vuren, 2001, pp. 119). In addition, cattle and bison display different foraging behaviors, with bison behaving more as energy maximizers. Bison are more likely than cattle to expend energy to obtain richer rewards at concentrated feeding sites that require long-distance movements (Van Vuren, 2001). Cattle behave as central place grazers, with foraging centered on water sources (Van Vuren, 2001). During a study of bison in Theodore Roosevelt National Park, Norland (1984) observed that bison did not center foraging activities around permanent water sources, but were instead highly mobile to utilize different water sources. Bison also used temporary water sources, went without water for at least one day, and utilized snow instead of water when available.

Van Vuren (2001) found that the location of bison foraging was relatively unaffected by the availability of water in comparison to cattle, and that bison were less likely to graze close to water. During his observations of the free-ranging herd of bison in the Henry Mountains in Utah, Nelson (1965) observed that "very little time was spent at the water hole. As soon as their water needs were satisfied, they immediately began grazing and moving away from the water and did not show a tendency to hang around the area as is common with cattle" (pp. 35–37).

The increase of vertical distance from water caused a steep decline in cattle foraging; however, the situation resulted in only a slight decrease in bison foraging (Van Vuren, 2001). While observing grazing behavior of cattle and bison in northeastern Colorado, Peden et al. (1974) observed that cattle selected areas for grazing that were located within swales or shallow depressions, where soil moisture is higher than in the surrounding upland vegetation where the bison grazed.

In a study on The Nature Conservancy's Tallgrass Prairie Preserve, Fuhlendorf et al. (2010) attempted to compare bison and cattle in a way that incorporated factors found within complex landscapes, including fire. The study found that both species had a high preference for regions that had recently been burned (Fuhlendorf et al., 2010), but the study found two key differences between the two species. The first was that cattle preferred regions with woody vegetation, but bison avoided them. The researchers felt that this behavior is related to thermal regulation, but that further investigation is required (Fuhlendorf et al., 2010). A second key difference was that "selection for sites closer to water was also greater in cattle than bison; in fact, bison spend less time near water than cattle" (pp. 16). Fuhlendorf et al. (2010) note that this difference "occurred in a well watered landscape and may be even more important in landscapes with greater distance between ponds and streams" (pp. 16).

The diet of the plains bison consists primarily of grasses, though bison will consume forbs and woody vegetation when their preferred vegetation is not readily available (Nowak and Paradiso, 1983; Foresman, 2001; Long, 2003; Burde and Feldhamer, 2005; Picton 2005). The study of the diet of bison, cattle, and sheep on short-grass vegetation in northeastern Colorado by Peden et al. (1974) found that bison have a greater preference for warm-season grasses, which are grasses that grow during the summer and mature in the late summer or fall. The study found that bison consumed more warm-season grasses than cattle or sheep, with these grasses making up approximately 80 percent of their diet except for during late winter and early spring. Peden et al. (1974) observed that the percentage of cool-season grasses, which are grasses that grow during the spring and flower in early summer, was in general greater in the diets of cattle than in bison. The study also found that the diets of sheep and cattle "frequently had relatively high proportions of forbs"; for example, warm- and cool-season forbs combined made up 72 percent of sheep and 47 percent of cattle diets in June, whereas the diet of the bison consistently contained less then 13 percent forbs (Peden et al., 1974, pp. 493).

On the National Bison Refuge, 88 percent of the bison's diet is made up of Idaho and rough fescue and bluebunch wheatgrass (Foresman, 2001). Meagher (1973) found in an analysis of rumen samples that sedges are the most important forage for bison in Yellowstone National Park, with sedges, rushes, and grasses making up 96 percent of their diet throughout the year.

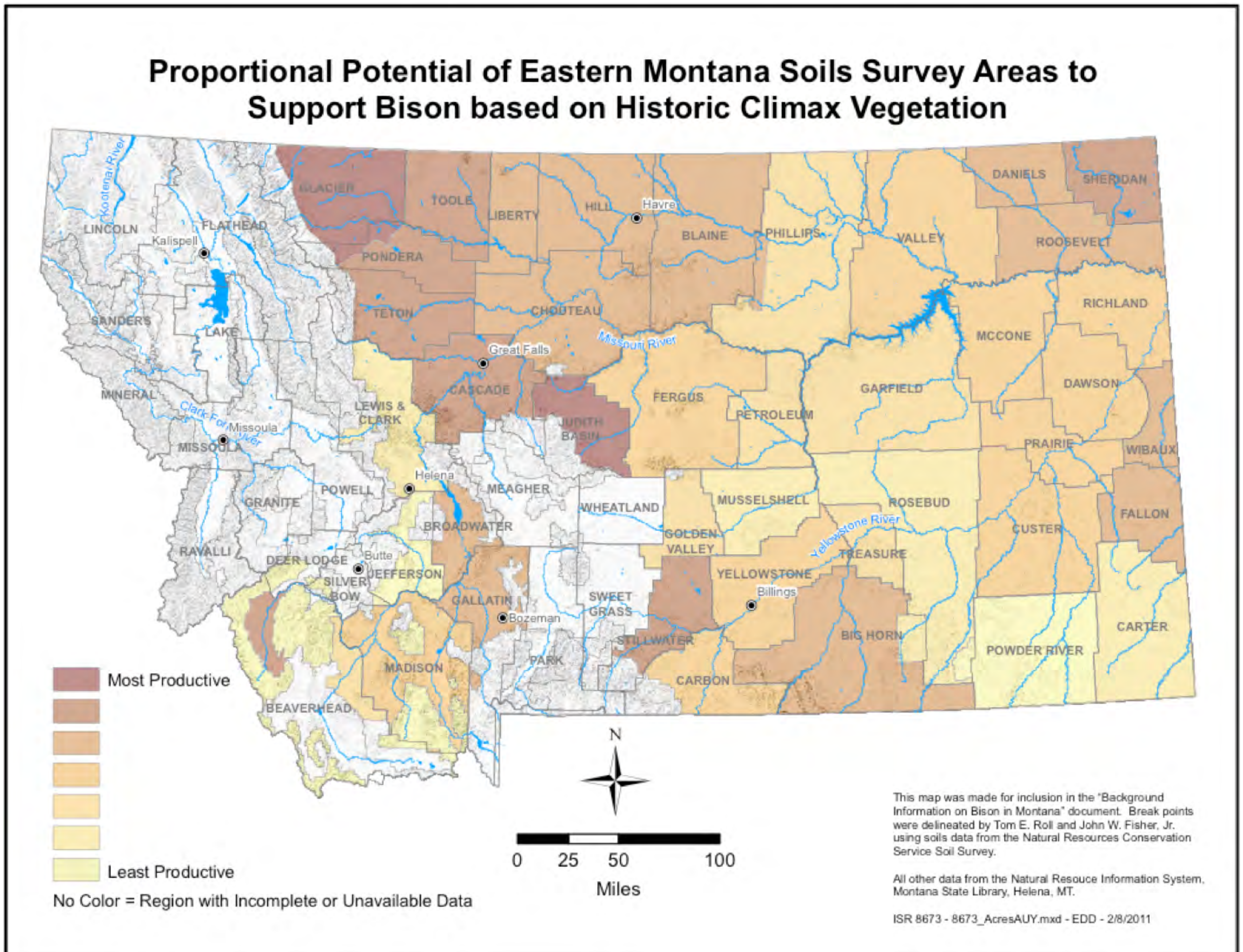
Bison's nutritional needs change seasonally and are related to the length of the day. A mature bison gains and loses weight cyclically, with weight loss occurring in the fall and winter, and weight gain occurring in the spring and summer (Feist, 1999). On average bison tend to lose 10 to 15 percent of their body weight during the winter (Feist, 1999). The shorter daily period of daylight during winter increases the concentration of melatonin that is produced by the pineal gland, which inhibits the secretion of growth hormone and thyroxin, and therefore lowers the bison's metabolic rate (Feist, 1999). This decrease in metabolic rate reduces the bison's forage intake to 1.4 to 1.8 percent of body weight, compared to the 2.0 to 3.0 percent intake that occurs during the remainder of the year (Feist, 1999). An experiment was conducted in which the calves of bison, yak, and Scottish Highland cattle were placed in a refrigeration chamber and temperatures were lowered to -22° F (-30° C). Each showed a marked increase in metabolic activity in an effort to raise body temperature, except for the bison, which lowered its metabolism. "As it got colder, bison slowed their metabolic rate" (Brink, 2008, pp. 172).

Bison have evolved the ability to plow away up to 18 inches of snow with their large low-hanging head in order to access the underlying vegetation (Meagher, 1978; Picton, 2005). This adaptation allows bison to effectively feed on natural sources during the winter season in conditions that may limit the forage ability of other wild ungulates and may require the diet of domestic livestock to be supplemented (Meagher, 1978).

In order to better determine agricultural stocking rates, animal grazing is measured by animal unit month (AUM). An animal unit (AU) is based on one mature domestic cow, which weighs about 1,000 pounds, and a calf that is as old as six months, or their equivalent. An AUM is the amount of forage required to support an AU for one month (NRCS, 1997). It is important to recognize that AUMs were developed as an agricultural tool for estimating stocking rates, and were not directly developed to determine the range impact of native ungulates. The *Montana Guide to Range Site, Condition and Initial Stocking Rates,* published by the Montana State University Extension Service, notes that "different animals also use different areas or forage species within a pasture. Thus AUM equivalents for sheep and wildlife have been omitted, because their food and habits differ from cattle" (Lacey and Taylor, 2005, pp. 3–4). Scarnecchia (1986) cautions against using AUMs to compare different species, because "animal-unit equivalents are simple values expressing the demand of animals in animal-units; they are not substitution rations" (pp. 471). Scarnecchia (1986) and Hobbs and Carpenter (1986) both caution against generalizing AUMs among species, and note that the differences in diet selection and forage behavior must be examined for each species.

In practice there are often differences in the actual capacity of the land to support native ungulate grazing than is indicated by AUM estimates due to the differences in foraging behavior between cattle and bison. It is also important to recognize the distinction between the ecological potential of a site and actual production of a site as influenced by the existing conditions. In order to determine the actual ecological potential of a site and its ability to support a bison herd, the following factors must be examined: the existing conditions of the range, the seasonal range and its utilization by all species, and how a site's potential would differ based on whether it was supporting a confined herd versus a free-ranging herd. The following process would need to occur to examine these factors. First, a rangeland assessment should be completed to examine the utilization of the site in specific areas and to estimate the utilization of the site by different ungulates. There would then need to be the completion of a habitat inventory and an estimation of carrying capacity. The seasonal ranges and the seasonal range use by different wildlife would need to be identified. Finally, the overall influences of other ungulates would need to be determined.

Map 7, created by T. Roll and J. Fisher Jr. (2010), is a projection of the proportional potential of regions in Montana east of the Continental Divide to support bison during normal precipitation conditions.



Map 7: Proportional Potential of Eastern Montana Soils Survey Areas to Support Bison Based on Historic Climax Vegetation. Map created by T. Roll and J. Fisher Jr. (2010) based on soil survey data from National Resource Information System and National Resource Conservation Service

Reproductive Biology

A female bison's ability to produce viable offspring is dependent on a number of factors including age, physical condition, and disease status. The age that a female first conceives varies among location and even within a herd (Reynolds et al., 2003). It is possible for female bison to conceive as yearlings and thus produce offspring at two years of age; however, this occurs in less than 4 to 5 percent of females (Berger and Cunningham, 1994a; Gates et al., 2010). It is more common for females to conceive at two years of age and thus produce their first calf when they are three years old (Reynolds et al., 2003). In Badlands National Park, Berger and Cunningham (1994a) observed that 58 percent of three-year-olds produced a calf. Prime breeding years differ between herds, but tend to range from four to ten years of age (Berger and Cunningham, 1994a; Aune et al., 1998; Gates et al., 2010). Under ideal conditions pregnancy rates for three-year-old cows will be about 70 percent or greater, and rates for prime age cows will normally average between 70 to 90 percent (Gates et al., 2010). Berger and Cunningham (1994a) found that calf production was highest from ages 5 to 13, with 75 percent of 10- to 11-year-olds annually producing calves. They observed that fewer than 30 percent of cows that were 14 and older produced calves (Berger and Cunningham, 1994a). Within Yellowstone National Park's northern herd, Aune et al. (1998) found that the highest reproductive potential occurred in females that were between four and eight years old; there was reduced reproductive potential in older females.

Male sexual majority also differs between locations, with some herds having a low percentage of yearling and two-year-old males becoming sexually viable (Reynolds et al., 2003). The majority of males begin to reach sexual maturity in their second or third year; however, bulls that are less than six years old tend to not yet possess the social maturity to successfully compete with other bulls for the opportunity to breed (Meagher, 1973; Reynolds et al., 2003; Picton, 2005). Bulls that are between seven and eight years old are the most competitive males, and therefore have the highest breeding success (Meagher, 1978).

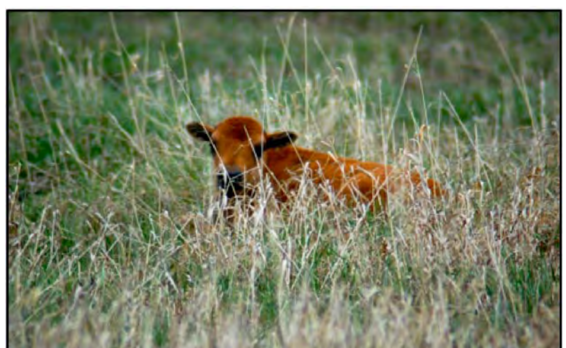
The breeding season of bison, which is referred to as the rut, tends to occur between July and September, with the majority of breeding occurring in July and August (Nowak and Paradiso, 1983; FWP and MNHP, 2010a). Cows are seasonally polyestrous, meaning that a female will come into heat multiple times during the breeding season if she does not conceive during the first cycle (Nowak and Paradiso, 1983; Long, 2003). During this time the males challenge one another to gain access to females (Berger and Cunningham, 1994a). Bulls determine the outcome of such challenges through a series of stages. The confrontation typically begins with posturing and parallel walking; it may advance to bluff charges, and finally charging and goring (Picton, 2005). While some interactions to establish dominance are determined without physical contact, when contact does occur there is often severe injury and occasional mortality (Dary, 1989; Geist, 1996; Picton, 2005). Picton (2005) noted that one study indicated that 50 percent of bulls showed

Bison bulls sparing. PHOTO CREDIT: D. LUTSEY; COURTESY GATES ET AL. (2010)

evidence of previously fractured ribs. Males also use bellows and vocalizations as threats and displays to other males during the rut (Berger and Cunningham, 1994a).

A male bison will attempt to breed with as many females as possible during each breeding season in order to increase the number of viable offspring that carry his genes (Long, 2003). Males do not form harems, but instead form temporary “tending bonds” or “guarding bonds” with females, allowing the bulls to breed with a number of females sequentially (Meagher, 1978; Berger and Cunningham, 1994a).

Gestation length and calving season may be highly variable, with bison achieving reproductive synchrony through gestation adjustments (Berger and Cunningham, 1994a). Gestation and calving seasons can be influenced by factors such as location and climatic conditions (Aune et al., 1998; Reynolds et al., 2003; Gogan et al., 2005). Gestation in bison can range from 9 to 9.5 months (Nowak and Paradiso, 1983; Reynolds et al., 2003; Picton, 2005; FWP and MNHP, 2010a). Within Badlands National Park, Berger and Cunningham (1994a) observed that the median of births occurred from May 2 to May 8, with 50 percent of births occurring within 19 to 23 days. Gogan et al. (2005) observed that within the two YNP herds the majority of births occurred in April and May, with 50 percent of all births occurring within 13 to 43 days and 80 percent of births occurring within 33 to 82 days. Jones et al. (2010) found that within the YNP herds the earliest newborn was seen in late March or early April each year and the last observed birth tended to occur in late May or early June. Similar findings of synchrony within the YNP herd were observed by Jones et al. (2010), who observed that 50 percent of births occurred within 15 days and 80 percent occurred within 32 days. Approximately 50 percent of births occurred by the 6th of May, 80 percent by the 16th of May, and 95 percent by the 27th of May (Jones et al., 2010).



BISON CALF. PHOTO CREDIT: S. ADAMS

Gogan et al. (2005) also observed that the availability of spring forage is a major factor in the timing of births. The effect that vegetation availability and nutrition may have on the timing of births is supported by the observation by Aune et al. (1998) that calving was earlier following a moderate winter and was delayed two weeks following a very severe winter. Aune et al. (1998) observed that most calves within Yellowstone National Park were born between mid-April and late May. Meagher (1973) reported that within Yellowstone most calving occurred in early May and was completed by late May, though indicated that as the population increases the calving season may extend. Pac and Frey (1991) found that the calving season is more prolonged than previously reported within the park, with most of the calving (76 percent) completed by early June. This evidence supports Meagher’s earlier observation. Calves that are born later have an increased risk of not surviving the following winter.

If vegetative cover is available, females will give birth in isolation; if cover is not available, isolation during birth is less frequent (Meagher, 1986). A cow delivers a single reddish tan calf, which is able to stand and suckle shortly after birth (Picton, 2005). Bison may produce twins; however it is extremely rare (Reynolds et al., 2003; Brodie, 2008). Aune et al. (1998) found that "bison birth sites were relatively clean and bison consumed membranes and occasionally the placenta" (pp. 69). Jones et al. (2010) also observed this behavior, noting that "bison birth sites covered small areas (e.g., 3 by 3 meters) and female bison meticulously cleaned birth sites by consuming all birth tissues, eating the vegetation, and licking the soil" (pp. 337). Calves begin to graze after their first month, and learn food selection through observing the herd (Picton, 2005). Most calves are weaned within 8 to 12 months (Long, 2003; Burde and Feldhamer, 2005).

Bison cows and calves. PHOTO CREDIT: E. AUSTIN AND H. JONES; COURTESY NPS

Demography and Population Dynamics

The rate of population growth is influenced by sex ratio, age structure, quality and quantity of forage and habitat, and the immigration and emigration rate combined with the reproductive and mortality rates (Gates et al., 2010). The survival rate of calves varies dramatically across different populations, whereas adult survival rates are generally higher and less variable (Brodie, 2008). Survival rates for prime age adults are approximately 95 percent, with the highest natural mortality rates occurring in calves and the oldest age class (Gates et al., 2010). Pac and Frey (1991) evaluated bison within Yellowstone National Park and found that the mean age was 4.96 and the oldest animal was 15 years old, which is consistent with other studies (Reynolds et al., 2003). Pac and Frey (1991) found that there were more males in the younger age class (1 to 4), more females in the older age class (5 to 9), and similar numbers of both sexes in the oldest age class (10 to 15). Studies of the central YNP herd by Geremia et al. (2009) found that there was reduced survival in this herd after 12 years of age. This is younger than the documented lifespan in other wild bison, and Geremia et al. (2009) speculate that it may be due to the geological features of this region of the park. Mortality may occur through predation, hunting, accidental drowning, parasites, and disease (Reynolds et al., 2003; Brodie, 2008).

Another major factor that causes mortality in bison is climate. Winters with above-average snowfall and long freezes result in mortality in bison, as these conditions reduce forage ability leading to poor animal condition and potentially death (Reynolds et al., 2003). Fuller et al. (2007a) found that population growth was negatively correlated with increased snowpack.

Population density can have an effect on survival, but usually only when it is combined with climatic pressures. Geremia et al. (2009) found that there was a significant decrease in the survival of adult females when the population in the central herd exceeded 2,000 to 2,500, with the decrease being intensified during winters of increased snowpack. Based on observation of the two herds within Yellowstone National Park, Fuller et al. (2009) discovered that bison tend to exhibit a spatial response to density dependence. They found that as increased density was combined with climatic variations, such as deep snowpack, there was increased pressure on resources. This increase in resource competition caused some of the central herd bison to emigrate to the northern herd, which had been reduced due to management practices.

Pregnancy and birth rates vary within different herds and are affected by multiple factors. Aune et al. (1998) found that within the northern YNP herd pregnancy rates were over 70 percent, which is high compared to many other free-ranging populations. "Although female bison get pregnant most years, they may not successfully calve or produce viable calves each and every year depending upon the severity of the previous winter" (Aune et al., 1998, pp. 69). Birth rates within YNP bison varied with age and disease status. Fuller et al. (2007b) found that birth rates for three-year-olds were 0.40 calves per female that had tested positive for brucellosis and 0.63 calves per female that had tested negative. Birth rates for females four years and older were 0.64 calves per female that had tested positive for brucellosis and 0.81 calves per female that had tested negative.

Another factor that can affect calf production rates is body condition of the female bison. On the National Bison Range, calf production has declined from the 1956 to 1987 historic average of 87 calves per 100 breeding age cows, to 32 calves per 100 breeding age cows (Borgreen, 2010). Borgreen (2010) found that decreases in body weight of female bison appear to be directly related to decreases in the production of calves. Borgreen (2010) notes that "from the historical trends, it would appear that the cause of anestrus during the breeding season is the result of body condition of cows at NBR, most likely due to range resources or other environmental factors" (pp. 60).

Fuller et al. (2007b) found that pregnancy and birth rates did not vary significantly with climatic changes, but the neonatal survival in the spring varied with both winter severity and warm-season growing conditions. This occurs because conception and gestation requires less energy than lactation (Fuller et al., 2007b). Calf survival varies drastically across different populations, but on average calf survival ranges from 40 to 90 percent, depending upon the severity of winter, predation pressures, and forage availability (Brodie, 2008; Gates et al., 2010).

Growth rate of bison populations is highly elastic to adult survival, with small changes in adult survival having large effects on population growth rate (Fuller et al., 2007b). Within Yellowstone National Park, Fuller et al. (2007b) estimated that the growth rate was λ=1.07, indicating an increasing population. Within free-ranging populations, growth tends to occur at a slower rate. The bison herd in Jackson, Wyoming, experienced a growth rate of 12.9 percent from 1969 to 2002 (Gates et al., 2010). Growth rate tends to be highest in captive herds where there is an absence of predation, supplemental feeding occurs, most or all of the surplus bison are culled annually, and there is a skewed sex ratio with a much higher number of females to males than in the wild (Gates et al., 2010). A herd that is managed under these conditions in Oklahoma experienced a growth rate of approximately 50 percent (Gates et al., 2010).

Ecological Roles

Bison and grizzly bear. PHOTO CREDIT: FWP

Bison are a keystone species within plains and prairie habitats, meaning they play an important role by influencing the plant and animal communities around them (Knapp et al., 1999; Truett et al., 2001; Gates et al., 2010). The impacts of large grazers such as bison can be both positive and negative—the key is how the species is managed on the landscape. For example, the grazing and wallowing behavior of bison result in the creation of specific environments, which contain plant communities that have a greater diversity than the surrounding region. This increase in plant diversity is utilized by other animals and increases the diversity of wildlife within the region (Foresman, 2001; Picton, 2005; Gates et al., 2010).

A study completed by Frank et al. (1998) found that the presence of large herbivores, bison, and elk within Yellowstone National Park increased the aboveground plant production by an average of 43 percent, thus dramatically promoting energy capture within the ecosystem (pp. 519). This study found that "ungulates stimulate allocation to shoot growth while simultaneously enhancing light levels, soil moisture, and nutrient availability" (Frank et al., 1998, pp. 518). Frank et al. (1998) note that "because animals are continually on the move, grazing at any site, although often intense, never lasts long. Furthermore, because ungulates tend to graze grasslands early in the growing season, when forage is the most rich in minerals, and then migrate off sites while conditions are still favorable for plant growth, defoliated plants are provided with both sufficient time and suitable conditions to regrow" (pp. 519). Frank et al. (1998) conclude that "in contrast to most terrestrial habitats, where climate is the preeminent factors determining primary production and ecosystem energy flow, ungulates play a major role in regulating these processes in grazing ecosystems" (pp. 519). Thus, "ungulates in grazing ecosystems do not simply respond passively to ecosystem gradients of forage characteristics; they actually modify vegetation structure, with the result that herbivores increase their own foraging efficiency" (Frank et al., 1998, pp. 518).

The grazing of bison and their presence in a region enhances the availability of nitrogen to plants by increasing nitrogen cycling and by altering the form in which inorganic nitrogen exists. This increase in available nitrogen increases the productivity of vegetation (Frank and Evan, 1997). Bison can stimulate increased biomass production in a grassland system by redistributing nitrogen and other nutrients through feces and urine deposition (Frank and Evan, 1997). The carcasses of bison also deposit nutrients into the soil and create a fertile area with higher biomass production as well as an increase in species richness and diversity (Towne, 2000).

Bison and prairie dogs have a mutually beneficial relationship. Prairie dogs utilize the same regions as bison; therefore keeping the grass short, and "the closer the blade is to the roots, the higher the percentage of protein and the lower the percentage of cellulose it contains" (Lott, 2002, pp. 128). This shorter vegetation attracts bison, whose droppings contribute needed fertilizer to the prairie dog colonies (Lott, 2002). Prairie dogs need lower vegetation to form colonies, and the grazing patterns of bison reduce forage height to levels that facilitate colonization by prairie dogs (Lott, 2002; Virchow and Hygnstrom, 2002; Gates et al., 2010).

Knapp et al. (1999) found that the grazing behavior of bison, which, in conjunction with wallowing and other ecological events such as fire, increase the diversity of the grasslands to provide suitable nesting habitat for a variety of obligate grassland nesting bird species (Gates et al., 2010). Grassland birds evolved alongside native grazers such as bison, and are dependant on the heterogenic mosaic landscape patterns that emerge from the grazing patterns of bison (Knopf, 1996). Some of the bird species that utilize bison-altered habitat are the upland sandpiper, grasshopper sparrow, mountain plover, McCown's longspur, ferruginous hawk, and long-billed curlew (Knopf, 1996; Gates et al., 2010).

Bison play an ecological role as an important food source for many predators and scavengers. Bison tend to turn and face an attacking predator, which increases the risk of injury to the predator (Meagher, 1978). Attacks on bison and bison calves tend to be infrequent and opportunistic, with predators often selecting older or weakened members of the herd or newborn calves (Varley and Gunther, 2002; Wyman, 2002). Historically bison carcasses supported wolves, grizzly and black bears, wolverines, bald eagles, ravens, coyotes, and swift foxes (Roe, 1970; Bogan, 1997; Truett et al., 2001). Wolf populations that were reintroduced to Yellowstone National Park that had not been exposed to bison in the past were able to adapt their behavior in order to utilize bison as a prey source, though bison have not become their preferred prey (Smith et al., 2000; Becker et al., 2009a, 2009b). In a study that monitored winter wolf kills in the northern range of Yellowstone National Park from 1995 to 2000, Smith et al. (2004) observed that in the early-winter study period bison made up approximately 2 percent of wolf kills. During the late-winter study period bison made up 6 percent of wolf kills.

In the northern range, bison have not become a significant prey source because elk, the preferred prey source, are more abundant and easier to hunt. Within central Yellowstone National Park, bison are utilized more frequently as a prey source due to the lower abundance of elk (R. Garrott, Montana State University, personal communication). In central Yellowstone National Park the kill rates of bison were primarily influenced by the abundance of bison calves and the severity of snowpack (Becker et al., 2009a, 2009b).

Becker et al. (2009a) were able to detect 606 bison and 151 elk killed by wolves within the Madison headwaters area from the 1996–97 winter to the 2006–07 winter.

Though the Sturgeon River Plains Bison Herd was reintroduced to Saskatchewan, Canada, in 1969, wolves did not begin to prey on these bison until the early 2000s (G. Vaadeland, Sturgeon River Plains Bison Stewards, personal communication). Predation began with one pack of wolves and there are now five packs that utilize the bison herd as a prey source (Vaadeland, personal communication). Prince Albert National Park has begun to study the predation of bison by wolves and is gaining a better understanding of this dynamic predator/prey relationship.

Bison evolved alongside other native ungulate species, such as elk, mule deer, and pronghorn. Knowles (2001) notes that "bison tend to ignore other ungulate species except when closely approached during a feeding bout. Interspecies aggression may be exhibited at this time but chase distances are typically very short as long as the other species exhibits flight behavior" (pp. 26). Due to the limited number of free-ranging herds, interactions between free-ranging bison and other native ungulates has not been extensively studied. Bison do co-exist with a number of native ungulates in parks, such as Yellowstone National Park.

Barmore Jr. (2003) examined the relationship between native ungulate species in the northern range of Yellowstone National Park between 1962 and 1970. Through combining his observations and relevant literature, he determined the amount of separation and the factors responsible for separation of the different species. Barmore Jr. (2003) found that the following ecological separations occurred between bison, mule deer, moose, bighorn sheep, and pronghorn antelope between 1962 and 1970, and probably during primeval times, based on major differences in four niche dimensions: spatial distribution, habitat selection, food habits, and tolerance of snow. Barmore Jr. (2003) observed that the factors responsible for the ecological separation of bison from mule deer and moose were major differences in spatial distribution, habitat selection, and food habits. He also observed that tolerance of snow was a factor responsible for the separation of bison and mule deer, but not bison and moose.

Barmore Jr. (2003) found that out of 953 bison-feeding observations, only 16 were in bighorn sheep range, and that bighorn sheep were never observed in areas consistently used by bison. Barmore Jr. (2003) notes that the factors responsible for the separation of bison and bighorn sheep were major differences in spatial distribution, habitat selection, and tolerance of snow.

The major factors responsible for the ecological separation of bison and pronghorn were major differences in spatial distribution, habitat selection, food habits, and tolerance of snow (Barmore Jr., 2003). Barmore Jr. (2003) notes that while historically bison may have ranged more extensively on the low-elevation pronghorn range, it is most likely that bison and pronghorn were separated ecologically by the major differences in their food habits and/or tolerance of snow. Barmore Jr. (2003) also notes that if the two species did occupy low elevations more extensively during the summer, a commensal interaction, in which one species benefits and the other neither benefits nor is harmed, may have occurred, as the bison's feeding on graminoids, which are flowering plants including grasses, would have increased the forbs and shrubs that are preferred by pronghorn. Fahnestock and Knapp (1993) noted that within tallgrass prairies, the grazing behavior of bison increased the soil temperature, availability of light, and soil moisture that was available to forb species. During observations of the grazing of bison and pronghorn on short-grass prairies in northeastern Colorado, Schwartz and Ellis (1981) found that the dietary overlap between bison and pronghorn was generally low. There was almost no overlap in August when bison consumed warm-season grasses and pronghorn warm-season forbs. The greatest amount of overlap occurred in March and October when the diets of pronghorn included 70 to 82 percent grasses.

Barmore Jr. (2003) observed that there was a considerable amount of overlap in the distribution and food habits of bison and elk on Yellowstone National Park's northern range; however, there were apparent differences in their habitat selection. Bison tended to be generally more specific in their habitat selection than elk, with elk feeding on a wider variety of topographic sites than bison. Barmore Jr. (2003) observed that both elk (75 percent of the time) and bison (91 percent of the time) primarily fed in grassland vegetation types from fall to spring. In the fall, elk and bison both preferred mesic grasslands and sedge-grass meadows, with elk showing more of a preference for sedge-grass meadows than bison (Barmore Jr., 2003). In the winter, elk shifted from sedge-grass meadows and mesic grasslands to xeric grasslands and sagebrush grasslands, whereas bison shifted from mesic grasslands to sedge-grass meadows, which were highly preferred (Barmore Jr., 2003). Gentle and level slopes were more heavily used and more highly preferred by bison than by elk during the fall and especially during the winter. This probably partly reflects the bison's greater tolerance of snow, which is normally deeper on level to gentle slopes where the bison's preferred sedge-grass meadows are most abundant (Barmore Jr., 2003, pp. 348).

In the spring, elk and bison both heavily used and highly preferred xeric grasslands. Both species also utilized sagebrush grasslands and mesic grasslands, though only elk preferred mesic grasslands. Bison continued to feed extensively on sedge-grass meadows, whereas elk did not (Barmore Jr., 2003). During the spring, south slopes were extensively used and preferred by both species, while ridgetops were extensively used and preferred by bison but not by elk (Barmore Jr., 2003, pp. 348).

Barmore Jr. (2003) notes that "niche overlap between bison and elk was minimal, and competitive interactions were probably nonexistent during the late 1960s due to differences in habitat selection and feeding behavior that largely reflected the ability of bison to cope with deeper snow than elk and thus feed on preferred high-producing mesic grasslands and sedge-grass meadows after the areas became unavailable to elk. Competition for food was essentially nil because utilization of graminoids (both cured and spring growth) was low over most of the area occupied by bison in winter and spring" (pp. 348).