

The references are ordered within categories named after factors that affect bison foraging. For example, foraging can be constrained by seasonal variation in food availability, therefore any articles pertaining to seasonal foraging constraints and/or preferences will be in the category, "**Seasonal Variation in Foraging Behaviour**".

Foraging Habitat Preferences

Reference: Coppedge, B. R., Leslie, D. M., & Shaw, J. H. (1998). Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management*, 51, 379-382. <https://doi.org/10.2307/4003321>

Summary: Three major grassland types were present in North America prior to European colonization: shortgrass, mixed-grass, and tallgrass prairies. Previous research on bison diets has been conducted on shortgrass and mixed-grass prairies, however, tallgrass prairie diets, because of habitat scarcity following farmland encroachment, have not been extensively studied. Coppedge *et al.* (1998) conducted an investigation of seasonal diet composition and preferences of mixed herd bison on a tallgrass prairie landscape using fecal analysis. Over four years, six fecal samples were collected each season from a mixed herd. Plant species composition was estimated from each sample. The fecal composition estimate was compared to an estimation of the plant species distribution of the tallgrass prairie to determine bison diet preferences. It was found that bison diets were primarily composed of grasses during every season. In most instances grasses were fed on in proportion to or slightly above their relative abundance on the landscape. Like grasses, sedges (grass-like plants) were grazed in proportion to their abundance, but were preferred over grasses in every season. Forbs (non-grassy herbs) were strongly selected against in all seasons despite their relative abundance when compared to sedges on the prairie landscape. Consumption of forbs and sedges peaked in spring, corresponding to the beginning of the growing season and the sprouting of highly nutritious shoots. Peak grass preference came in winter, corresponding to a relative decrease in all other forage options due to colder weather constraining forage availability. The authors propose bison cows have extreme sedge preference in mixed herds as they require nutritional supplements to support lactation and calf-rearing efforts. This article is significant as it outlines mixed-herd feeding preferences on tallgrass prairie, something not done before. It also suggests these preferences increase prairie diversity as ungrazed forbs are relieved of graminoid competition, increasing their growth and productivity rates.

Contribution: This article is significant as bison diet preference composition on tallgrass prairie had not previously been extensively studied. The authors discovered how bison diets fluctuate with regard to seasonal variation in vegetation composition

within tallgrass prairie habitats. I included this article in my literature review as it highlighted this understudied habitat that was at one time so important to the ecological function of American bison. One thing to keep in mind, however, is that the authors studied mixed herds of bison only, and do not distinguish between male and female foraging habits like other studies have done.

Reference: Coppedge, B. R., & Shaw, J. H. (1998). Bison grazing patterns on seasonally burned grassland prairie. *Journal of Range Management*, 51, 258-264. <https://doi.org/10.2307/4003408>

Summary: North American prairies and bison evolved in tandem with wildfires for millennia. Previous observations have recognized bison preferentially foraging in recently burned areas when other habitat was equally available. Coppedge and Shaw (1998) noted that no previous observations had taken into consideration sexual segregation among bison groups, and thus investigated how different social groups forage on burned grassland. A fire regime was initiated, with different randomly selected portions of The Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma being burned seasonally from summer 1993 to fall 1994, excluding the winter season. Bison herd location, size, and type (bull or mixed herds) was recorded 4-12 times per month within the timespan of the fire regime. Both herd types preferentially foraged on burned areas more often than unburned areas, with a few differences. Mixed herds preferentially selected recently burned areas more often than bull herds, while also showing significant avoidance for unburned areas when burned foraging grounds were available. Bulls showed a higher preference for unburned habitat than mixed groups, but still generally preferred burned areas. Burned habitat was most preferred in summer, followed by fall and spring. Temporal grazing trends also indicated that bison only grazed older burns in proportion to their availability, or outright avoided them, presumably because they lacked young, nutritious plant growth. The authors suggest bison foraging preference for burned grassland correlated with nutrient availability. The forage of the study range was most nutritious in spring, so introducing fires in summer and fall replaced less nutritious forage with more palatable sprouts that bison prefer, replicating spring-time conditions. Herds would avoid older burn areas as they did not contain as many nutrient-rich sprouts as a newer burn. This article is significant in that it identified burn patch size and age as two primary factors in bison burned patch preference.

Contribution: This article demonstrates differences in the sex-specific foraging habits of bison herds when fire is introduced back into their habitat. It is significant in that this

research is the first of its kind to take into account sexual segregation when foraging trends are observed on burned grassland. They also identified two primary drivers in bison foraging preference on burned grassland: patch size and age. I included this article in my literature review as it provides further insight into the sexually segregative behaviour of bison herds as well as showcasing foraging trends that were likely present in bison before European extermination.

Seasonal Variation in Foraging Behaviour

Reference: Hecker, L. J., Coogan, S. C. P., Nielsen, S. E., & Edwards, M. A. (2021). Latitudinal and seasonal plasticity in American bison *Bison bison* diets. *Mammal Review*, 51(2), 193-206. <https://doi.org/10.1111/mam.12229>

Summary: Dietary niches, or what organisms eat when food is available, are extremely important in understanding animal foraging behaviour. Hecker *et al* investigated the kinds of foods female American bison exploit (grasses, herbs, and tips of woody plants) and what macronutrients those foods contained to estimate how climate and latitudinal changes affect a bison's dietary niche. A literature review was conducted, finding 26 articles describing bison diet composition across North America. Articles describing the same bison group were collated together. Literature for macronutrient content (protein, carbohydrates, and lipids) contained within grasses, herbs, and browse (tips), respectively, was also found to estimate macronutrient intake and preference of bison. Bison females' average diet contained 85% grasses, 8.5% herbs, and 6.5% browse. As such, carbohydrates made up the vast majority of female bison macronutrient intake, with proteins and lipids making up a much smaller share. Despite data from across the continent being included in the review, the data suggested all bison shared a very narrow range of diet preference and nutrient intake. During summer, bison dietary niches appeared to expand as plant productivity increased. Grasses still composed over 80% of their diet. Colder weather at higher latitudes corresponded with increased consumption of browse to obtain more lipids, likely in response to requiring greater energy stores and fat reserves to stay warm and active. The review discovered an alarming lack of data of bison foraging behaviour during autumn and early winter, and while bison diet composition and macronutrient intake suggest a largely grass-based diet likely supplemented at higher latitudes with browse to increase fat reserves, further research is required. The diet of the American bison shows they have a narrow diet niche, similar to other grazing ungulates, and can adapt to the availability of local forage to meet their nutritional requirements.

Contribution: This review article collated data from bison groups across North America to better understand the extent of bison dietary niches across geographic distributions. Seasonal and latitudinal changes appeared to influence what bison ate and what macronutrients they required in their diet while not completely restricting bison diet. This review builds on the already understood knowledge of bison diet composition, expanding it into macronutrient makeup of common forage items and their dietary requirements in females. This article is important to my topic as bison dietary and macronutrient requirements are likely influenced by seasonal changes and latitude, influencing overall foraging behaviour.

Reference: Jung, T. S. (2015). Winter diets of reintroduced bison (*Bison bison*) in northwestern Canada. *Mammal Research*, 60, 385-391.
<https://doi.org/10.1007/s13364-015-0240-2>

Summary: Bison are able to digest forage low in protein and high in fibre, offering them an increased ability to adjust to seasonal variation in forage availability. There also exists variation in male and female diets, with males preferring less digestible forage than females. Jung (2015) predicted that male and female wood bison diets would differ significantly during early and late winter, as differential sex-specific energy requirements would cause diet segregation. Seven fecal samples were collected in March, 1998, and a further six were collected in December. The samples were examined to identify the diet composition of the origin bison. It was found that diet breadth of both sexes was much larger than had previously been observed for herds living at lower latitudes. In the north, there was less reliance on sedges and rushes, likely due to their comparative rarity at higher latitudes. It appeared that wood bison were making use of a greater variety of plant species to meet cold weather nutritional demands, while still showing significant preference, albeit much less so than southern latitude groups, to typical bison favourites like sedges and rushes. There was also no difference in late-winter diets between the sexes, despite observations showing they were segregated this time of year. Jung suggested this pattern was caused by restrictive forage availability, as snow depth could have prevented successful foraging, causing both sexes to consume forage in proportion to its availability to meet energetic costs, regardless of diet preference. Differential diet requirements were therefore not found to cause sexual segregation during late winter. Diet differences were seen in the early winter, although this was expected as each sexes preferred forage was more widely available. This article demonstrates bison dietary breadths can be more extensive than previously thought and can be constrained by environmental pressures.

Contribution: This article is significant in that it showcases how adaptable bison are to seasonal variation in forage availability, with diet breadth increasing in response to limited forage availability. Further, forage limitations can be so extreme that they overcome bison sex-specific diet preferences even while males and females are segregated. Normally, male and female diets do not coincide unless they are sharing the same habitat, like during rut. I chose this article to outline how adaptable bison can be to limited forage choice, to the point where diet preferences can be eclipsed even while males and females are segregated.

Diet Choice While Sexually Segregated

Reference: Berini, J. L., & Badgley, C. (2017). Diet segregation of American bison (*Bison bison*) of Yellowstone National Park (Wyoming, USA). *BMC Ecology*, 17(1), 27. <https://doi.org/10.1186/s12898-017-0137-9>

Summary: American bison spend most of their adult lives sexually segregated, leading to differences in grazing behaviour based on sex. This study investigated how sex-specific differences in composition, quality, and breadth of American bison diets vary between short and long time periods on the Northern and Central ranges of Yellowstone National Park. ^{15}N and ^{13}C isotopes were obtained from 60 fecal (collected during mating season over 10 days) and 40 collagen (from carcasses of bison that died no longer than 36 months prior to the study) samples from male and female bison to determine diet quality (^{15}N) and diet breadth (^{13}C) during those time periods. It was found that in both ranges bison diet varied significantly between the sexes. Females preferred higher quality forage while males ate a greater variety of forage (greater dietary breadth). Females require higher quality diets than males to undergo pregnancy and lactation, while males' large sizes mean they must eat a lot to maintain their bulk and therefore must forage whatever plants are nearest to them, regardless of quality. During short time periods like mating season, bison on the Central range had more pronounced diet segregation than they did during long time periods (multiple years). Over long time periods males and females consume a similar array of plants, but during short-term observation female and male forage preference was more distinct. This relationship was reversed on the Northern range, showcasing a different forage abundance and quality in that area. This study was significant because it showcases bison diet preferences vary by sex. Further, it shows that diet segregation behaviour can result from varying temporal (like time of year limiting or promoting high and low quality plant species growth) and spatial (amount of plant species found in an area) factors.

Contribution: This article highlights the importance of understanding spatio temporal heterogeneity when studying ungulate foraging behaviour. It cannot be assumed that all geographic locations in an ungulate's range contain similar quality forage. Berini and Badgley also found evidence supporting the previously discovered distinction between male and female bison forage quality preferences, in doing so ensuring future studies can be undertaken to determine nutritional component (like carbohydrates and protein) preferences and requirements of each sex's diet. As this article describes sexually segregated diet preferences in bison, it aligns perfectly with my topic looking at bison grazing behaviour.

Reference: Mooring, M. S., Reisig, D. D., Osborne, E. R., Kanallakan, A. L., Hall, B. M., Schaad, E. W., Wiseman, D. S., & Huber, R. R. (2005). Sexual segregation in bison: A test of multiple hypotheses. *Behaviour*, 142(7), 897-927.
<https://doi.org/10.1163/1568539055010110>

Summary: Sexual segregation, where males and females of a species form separate groups for most of the year, is a common behaviour in bison. It is thought that if sexual segregation confers a fitness advantage by improving individuals' physical health, it should be more pronounced at the time of year when habitat choice and energy requirements between males and females differ the most. Mooring *et al.* (2005) recognized this time of year as being prior to rut, and thus looked at habitat use, diet preferences, and activity budgets of cow and bull herds prior to and during the mating season. Fecal samples were examined for their nitrogen content to determine relative diet quality of both groups, with higher nitrogen concentrations correlating to higher quality diets in terms of digestibility and energy content. Activity budgets and habitat preferences were determined by observing both herd types. Data was collected from early June and July (pre-rut) and late July into August (during rut). There was no difference found in bull and cow herd preference for water proximity, tree cover, ruggedness, or openness of habitat. Bull groups did tend to choose habitat containing more invasive grass species, presumably due to their predilection for lower quality forage. Bull groups were also considerably smaller than cow groups, suggesting lower quality diets were offset by higher forage availability per individual. Fecal analysis showed male and female bison diets were distinct pre-rut, but were not significantly different during. As bison herds converged during rut, this result was unsurprising. Sex-dependant activity budgets were found to differ significantly only during rut, as males spent more time tending to females and fighting competition rather than foraging. This article is significant as it provides evidence for sexually dimorphic digestive

physiology being the major driver of sexual segregation in bison, not sex-specific activity budgets.

Contribution: This article is significant because it suggests sexual segregation is driven by sexual dimorphism and differential digestive physiology. Further, sexual segregation was found to maximize individual fitness of males and females, as males consuming lower quality forage ensured the availability of higher quality forage for females who have less robust digestive tracts. Increasing female fitness also facilitated calf survival through the production of more nutritious milk. I included this article in my review as it tested multiple hypotheses for the development and ramifications of sexual segregation in bison, showing that diet preference is the primary driver of segregation.

Reference: Post, D. M., Armburst, T. S., Horne, E. A., & Goheen, J. R. (2001). Sexual segregation results in differences in content and quality of bison (*Bos bison*) diets. *Journal of Mammalogy*, 82(2), 407-413.
[https://doi.org/10.1644/1545-1542\(2001\)082%3C0407:SSRIDI%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082%3C0407:SSRIDI%3E2.0.CO;2)

Summary: Bison males and females segregate by sex for most of the year. A number of hypotheses have been proposed explaining why the behaviour exists, including calf protection and diet selection, though none have been confirmed. Post *et al.* (2001) investigated the diet quality and composition of socially grouped bison to determine whether sex-specific diet preferences drive sexual segregation. Fecal samples were collected once a month for 21 months from bulls, cows, juveniles, and calves, and were examined for their nitrogen concentrations and their ratio of C₃:C₄ plant composition. There was no observed difference in the C₃ composition of cow, juvenile, and calf diets, likely because their close proximity in female herds meant overlapping diet selection. Bulls ate greater amounts of C₄ plants than all other groups, likely due to their preference for lower quality, less digestible forage. Peak consumption of C₃ plants in all groups occurred in April, coinciding with the beginning of growing season for those species, and in November for unknown reasons. Fecal nitrogen concentrations were also higher in April, indicating a higher quality diet for cow herds was obtained by grazing newly sprouted C₃ plants. There was no apparent increase in nitrogen content of feces in November. Cows and younger bison preferentially consuming C₃ plants aligns with previous research into bison physiology. C₃ plants are easily digested compared to C₄, and since smaller bison have shorter and less robust digestive tracts they preferentially select more digestible forage. In contrast, males, owing to their larger gut size, have physiology that favours consuming less digestible forage. This behaviour leaves more digestible forage for females whose health is intrinsically tied to the fitness

of males' offspring. This article's significance arises from its assertion that sexual segregation reduces competition for limited high quality resources.

Contribution: This article is significant because it suggests that both males and females maximize their fitness through diet segregation caused by geographic separation. Males preferring lower quality diets reduces competition for more nutritious and easily digestible forage that females then use to keep themselves and their calves healthy. The paper suggests that as all individuals involved benefit from sexual and diet segregation, the behaviour is perpetuated. I included this article in my review as it addressed the potential fitness benefits acquired through sexual and diet segregation, closely linking foraging success with reproductive benefits and survival.

Foraging Activity Budgets

Reference: Bergman, C. M., Fryxell, J. M., Gates, C. C., & Fortin, D. (2001). Ungulate foraging strategies: Energy maximizing or time minimizing? *Journal of Animal Ecology*, 70, 289-300. <https://doi.org/10.1111/j.1365-2656.2001.00496.x>

Summary: Ruminants are constrained in their energy intake by their morphology and physiology, as well as the energy and nutritional content of their diets. Bergman *et al.* (2001) investigated how wood bison foraged within the constraints of forage availability and quality, to determine whether bison pursue energy maximizing or time minimizing grazing strategies. To test the forage availability constraint, five trials were performed between June through August, 1994, where three different yearling bison were fed pre-measured but functionally unlimited amounts of forage from the surrounding landscape twice daily for four days. The forage quality constraint was tested by creating three replicate paddocks in a natural meadow where bison foraging decisions were monitored with regard to their forage patch biomass preference. In both experiments, the energy content of the consumed forage was estimated. From the unlimited forage trials, it was discovered that forage digestibility was negatively associated with forage biomass, and bison consumed proportionally less forage as biomass increased. This indicated that at instantaneous to short time scales and with unlimited forage availability, bison tend to be energy maximizers. When forage quantity was limited, however, bison preferred patches of higher biomass and consumed forage inversely to their digestibility (preference to high biomass, low energy patches). This indicates that at longer temporal scales, bison are time minimizers. In the wild, forage availability constrains bison diet choice more often than forage quality considerations, thus, overall, bison were found to

be time minimizers. The authors suggest behaviour evolved in an environment where time bison spend foraging conflicts with other activities that contribute to overall fitness, like watching for predators or following a herd. These findings were significant in that they disprove the widely held belief that all ungulates utilize energy maximizing strategies rather than time minimizing strategies while foraging.

Contribution: This article provides evidence against the widely held belief that all ungulates utilize energy maximizing foraging strategies to maintain their larger body masses. Further, it predicts that at longer time scales, biotic factors that influence an organism's fitness, such as predation risk and herding behaviour, contribute more than was once realized to how ungulates budget their time and energy towards daily tasks like foraging and vigilance. This article provides me with background for how time minimizing foraging strategies could have evolved, and the relative importance of forage availability and quality in such strategies.

Reference: Fortin, D., Fryxell, J. M., & Régis, P. (2002). The temporal scale of foraging decisions in bison. *Ecology*, 83(4), 970-982.
[https://doi.org/10.1890/0012-9658\(2002\)083\[0970:TTSOFD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0970:TTSOFD]2.0.CO;2)

Summary: Classical foraging theory predicts that animals will maximize their rate of energy intake over long periods of time, however, the model often fails to consider other activities that affect foraging behaviour. When observing bison, this constraint becomes evident when vigilance and resting behaviours limit daily forage intake. Time to ingest and digest must also be considered. Fortin *et al.* (2002) predicted optimal diets and compared them with the observed diets of 220 plains bison for six month-long periods spanning 1998. Optimal diets were determined using a model, and observed diets were calculated by estimating the total amount of biomass grazed in evenly spaced 1 m² quadrats. The model predicted bison would maximize their energy intake by specializing on a different plant species every season. It was found that, contrary to the established principles of classical foraging theory, bison displayed patch preference that maximized short-term over long-term gains. They chose against the predicted most profitable graze species of each season and instead opted for a single, favoured grass species every season. It appeared that bison made short-term foraging decisions hierarchically, first maximizing their energy intake by consuming their favourite food, then selecting patches based on forage height. The time saved by selecting such a diet appeared to be small, so the authors were unsure of what fitness benefit bison gain by doing this, though they proposed that unpredictable herd movements inducing an “eat-while-you-can” mentality could select for this kind of strategy. They also predicted

that bison preferentially fed on a single species year-round to maintain their gut microbiome and ensure maximum energy gains when consuming forage leading up to an important event like rut. Overall, bison preferred rapid energy acquisition even when such behaviour would impair long-term benefits, a significant finding as it contravenes established principles of classical foraging theory.

Contribution: The significance of this article comes from its findings conflicting with classical foraging theory. This suggests that when observing animal behaviour, or at least bison behaviour, more descriptive models need to be implemented to properly predict and study foraging decisions like diet preference. Bison selecting diets based on short-term gain was also surprising as cattle, considered close ecological substitutes, maximize *long-term* gains when foraging, showcasing there can be significant foraging differences even amongst closely related species. I included this article in my review as it illustrates how and why bison prefer foraging decisions that maximize short-term gain.

Reference: Rutley, B. D., & Hudson, R. J. (2001). Activity budgets and foraging behavior of bison on seeded pastures. *Journal of Range Management*, 54(3), 218-225. <https://doi.org/10.2307/4003237>

Summary: Ruminants, including bison, alternate between foraging and resting activities periodically throughout the day. Partial activity budgets have been assembled, however, a comprehensive, seasonal description of bison daily activity budgets has never been compiled. Rutley and Hudson (2001) documented seasonal behaviour changes of six captive bison in seven trial periods spanning June 1994 through December 1995 to detect seasonal changes in foraging bout length and frequency. The animals were observed for multiple 24 hour periods each trial, and their behaviours were split into ten categories: Active foraging, moderate foraging, consumption, ruminating, standing, bedding, sleeping, drinking, walking, and playing. Resting and foraging constituted the majority of daily bison activities. Time spent resting and foraging changes seasonally. Foraging and resting bouts in the summer were observed to be less defined as bison never spent extended amounts of time in either activity. Energetic activity continued until sundown when bison settled for the night. In fall, grazing periods became less numerous and more regimented as clear foraging bouts were always observed before dawn, at midday, into the evening, and at midnight. Winter patterns were similar to fall patterns except the three shorter daytime foraging bouts were condensed into two longer bouts. Winter saw significantly more foraging and less resting than summer. From the activities observed, the authors concluded that bison are able to adjust their grazing behaviour in accordance with shifting seasonal nutritional requirements.

Switching between different behaviours multiple times a day is known as being polyphasic, and the authors suggested that while this was an appropriate description of summer and fall foraging behaviours, winter foraging behaviour was distinctly triphasic with two major bouts during the day and one at night. An ethographic description like this had never been undertaken before, making this article significant in the study of bison foraging behaviour.

Contribution: The authors described seasonal variation in behaviours of captive bison, something that had never been fully examined before. From there, they were able to note typical daily trends, like an increasing amount of time spent foraging as colder temperatures arrived. While the authors mainly intended for their data to be used to implement feeding timetables for captive-bred bison, their activity budgets can still be used to approximate the foraging schedules of wild populations. I included this article in my review as it summarizes seasonal variation in bison activity budgets and showcases how time spent foraging is seasonally dependent.