

SEXUAL SEGREGATION RESULTS IN DIFFERENCES IN CONTENT AND QUALITY OF BISON (*BOS BISON*) DIETS

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We examined diets of bison (*Bos bison*) bulls, cows, juveniles, and calves to determine differences in quality of diets between groups. Our results showed that bulls had a significantly higher proportion of C₄ grasses in their diet than cows, juveniles, or calves. Diets of calves were of higher quality than diets of bulls, cows, or juveniles. Our results provide support for the sexual dimorphism–body size hypothesis of sexual segregation in large ungulates.

Key words: bison, *Bos bison*, diet composition, diet quality, sexual segregation

An understanding of diet composition is important to the study of a number of areas of animal biology. In particular, it has been suggested that knowledge of diet composition is important to understanding sexual segregation as it occurs in large ungulates (Main et al. 1996). Any hypothesis that explains sexual segregation behavior must rely on the assumption that despite using different parts of the range, all groups within a population have access to adequate diets.

Main et al. (1996) outlined 3 general hypotheses that ought to explain the phenomena. The reproductive-strategy hypothesis states that ecological factors are responsible for sexual segregation in large ungulates. This hypothesis predicts that males should use areas of abundant and nutritious resources. Further, it predicts that females should use areas that provide a predictable supply of resources and safety for offspring even if the result is a decrease in nutritional quality compared with what is available elsewhere within the range.

The social-factors hypothesis states that factors such as offspring survival or male–male competition drive sexual segregation. This hypothesis makes no direct predictions about diet choice. However, implicit in this hypothesis is the assumption that all groups have access to equally nutritious diets.

The sexual dimorphism–body size hypothesis states that physiologic factors related to nutrition create sexual segregation. This hypothesis predicts that males will use areas of lower-quality forage even when higher-quality forage is available. Further, it predicts that females will use areas of higher-quality forage to meet nutritional demands of pregnancy and lactation.

Ruckstuhl (1998) proposed a 4th hypothesis, which we refer to as the foraging-behavior hypothesis, to explain the sexual segregation of ungulates. The foraging-behavior hypothesis states that sexual dimorphism leads to differences in time budgets and movement patterns of males and females. Such differences make it difficult for males and females to stay together as a group, and sexual segregation is the result.

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Like the social-factors hypothesis, this hypothesis makes no specific diet-related predictions. Therefore, we assume that under this hypothesis all groups would be expected to have access to equally nutritious diets.

In January 1995, Tieszen et al. (1998) initiated a multisite study of the diet patterns of bison cows. In April 1996, we expanded the portion of the study being conducted on Konza Prairie Research Natural Area in Kansas to include an analysis of diet patterns of bison bulls, juveniles, and calves. Our goal was to investigate composition and quality of diets of social groups of bison to provide data useful to understanding sexual segregation in large ungulates. We also were able to study changes in diet choice and quality as group membership changed.

MATERIALS AND METHODS

Our study was conducted on the Konza Prairie Research Natural Area in Kansas ($39^{\circ}1'N$, $96^{\circ}6'W$), where, over the course of our study, an average of 220 bison grazed 949 ha. To determine diet choice and quality, we collected fecal samples on the 15th of each month (± 3 days) from April 1996 through December 1997. In each month, we collected samples from 3–6 individuals in bull, cow, juvenile, and calf groups. We located groups of animals and observed them until feces were deposited on the ground. Samples were collected within 30 min of deposition and stored on ice for ≥ 6 h until sample collection was completed for the day. Samples were dried at $60^{\circ}C$ to a constant weight. Dried samples were shipped to Augustana College, where they were processed and analyzed for $C_3:C_4$ ratio of plants and percentage fecal nitrogen.

The $C_3:C_4$ ratio of plants in the diet was assayed with an isotope-ratio mass spectrometer (Tieszen et al. 1998). Stable carbon-isotope ratios provided a reliable tool for the assessment of diet composition (Ambrose and DeNiro 1986; Tieszen 1991; Tieszen and Fagre 1993; Tieszen et al. 1979). In addition to providing a measure of diet composition, the analysis of $C_3:C_4$ ratios also provided a measure of diet quality. Several studies have shown that C_3 plants are higher in dry matter digestibility than C_4 plants (Hill et al. 1989; Wilson and Hacker 1987; Wilson and Hat-

tersley 1989; Wilson et al. 1983). Therefore, diets with a higher C_3 component should contain more available energy.

Nitrogen concentrations in fecal material were determined by gas chromatography (Tieszen et al. 1998). Nitrogen content of fecal material has been used as a measure of forage quality (Leslie and Starkey 1987; Wehausen 1995). However, it is not an absolute measure of diet quality (Hobbs 1987; Robbins et al. 1987). Therefore, in the present study, fecal nitrogen provided a relative measure of diet quality between groups but was not a measure of absolute quality. We assumed that no difference in digestibility of N occurred among our sex and age groups.

In concordance with the information available for large ungulates in general (Main et al. 1996) and bison in particular (Coppedge and Shaw 1999; Lott 1981; McHugh 1958), we observed segregation of male and female bison except during rut. Outside rut, we found cows, calves, and juveniles in 1 large group or several smaller groups, as is typical for the species. Bulls age ≥ 7 years old usually were observed alone or in small groups of 2 or 3 individuals. Bulls age 3–6 years old were most often found in groups of 5–10 individuals and seldom were seen alone.

All individuals in the herd were assigned to a specific age group using the following criteria. Viable sperm is present in male bison ≥ 3 years of age (J. Vestweber, pers. comm.). Further, it is at about 3 years of age that males were observed to leave the cow-calf group and join a bull group. Therefore, males ≥ 3 years of age were assigned to the bull group. Most female bison give birth to their 1st calf in their 3rd year (Green 1986; Lott 1981). Thus, females ≥ 3 years of age were assigned to the cow group. Animals from 14 months to 3 years of age were assigned to the juvenile group. In bison, weaning is not complete until the summer following their birth (Green 1986); therefore, animals 2–14 months of age were assigned to the calf group.

In most cases, we were able to identify the individual from whom each fecal sample was collected. However, in July–November of each year, samples collected from calves could not be assigned specific individuals because they had not yet been given an ear tag by which they could be uniquely identified. During that period, care was taken to ensure that, in each month, samples were taken from 3–6 different calves.

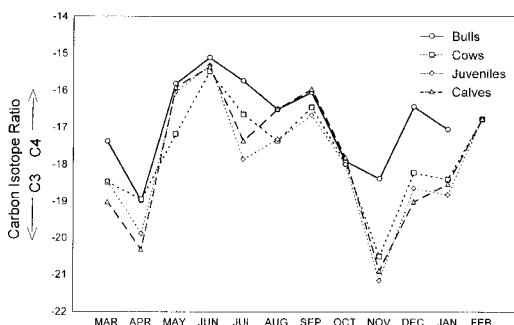


FIG. 1.—Carbon-isotope ratios in diets of bison bulls, cows, juveniles, and calves. Peaks in consumption of C_3 plants occurred in April and November.

Samples were not available from calves <2 months old because dams would not allow us close enough to collect fecal material. In any case, calves from birth to 2 months of age were assumed to be gaining nutrition solely by nursing because calves do not graze extensively until about 2 months of age (Green et al. 1993).

Statistical analysis was accomplished with the use of Statistical Analysis Software (SAS Institute Inc. 1997). A general-linear-model procedure was used to determine differences in $C_3:C_4$ ratio and fecal nitrogen within each month and over the entire study period (in all cases $d.f. = 3$). A least-significant-differences test was used to determine differences in diet content and quality between groups within each month. Percentage nitrogen data were log transformed prior to analysis and converted back to a percentage for presentation. Repeated-measures procedures were not used because the same animal was seldom sampled in successive months. Where the same animal was sampled in successive months, fecal samples collected 30 days apart were assumed to result from the consumption of different meals.

RESULTS

When summed across groups, a month-by-month comparison of $C_3:C_4$ ratio showed no difference between the 2 years of the study. Thus, data from both years of the study were combined before $C_3:C_4$ ratios were compared between groups. An analysis of diet choice by month showed that in some months there was no difference

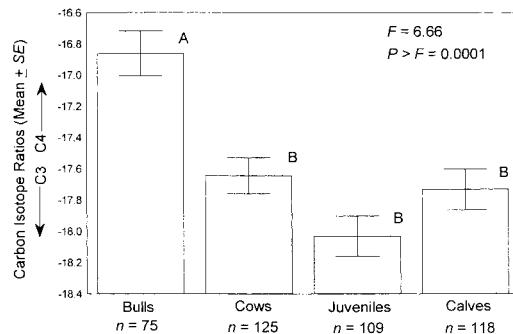


FIG. 2.—Ratios of consumption of $C_3:C_4$ plants over all months from April 1996 to December 1997. Bars with different letters indicate significant differences in ratios between groups.

in the ratio of $C_3:C_4$ plants in the diets of bulls, cows, juveniles, and calves (Fig. 1). However, in every month, the diet of the bull group contained as great or greater a proportion of C_4 plants as any other group. The ratio of $C_3:C_4$ plants in the diet of bulls differed from other groups in March ($F = 8.73$, $P = 0.0001$), July ($F = 8.801$, $P = 0.0002$), November ($F = 18.44$, $P = 0.0001$), December ($F = 10.50$, $P = 0.0001$), and January ($F = 8.27$, $P = 0.0001$; Fig. 1). In April, diets of bulls and cows contained a greater proportion of C_4 plants than diets of juveniles and calves ($F = 8.06$, $P = 0.0003$). When summed across months and years, diets of bulls contained more C_4 plants than diets of other groups ($F = 6.66$, $P = 0.0001$; Fig. 2). Thus, the diet composition of bulls differed from the diet composition of cows, juveniles, and calves.

Two peaks in consumption of C_3 plants occurred in all groups in April and November (Fig. 1). In April the peak coincided with the onset of the growing season at the Konza Prairie Research Natural Area, and in November the peak coincided with a 2nd peak in production of C_3 plants that occurred in autumn (Tieszen et al. 1998).

When summed across groups, the month-by-month comparison of fecal nitrogen content showed no difference between the 2 years of the study. Thus, data from both

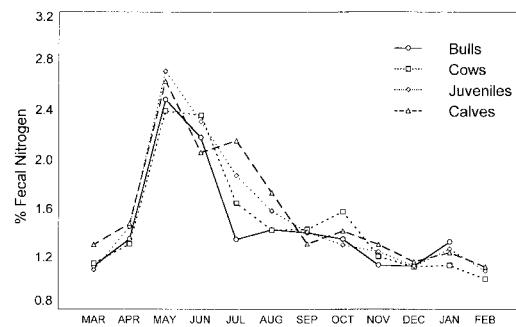


FIG. 3.—Fecal nitrogen in diets of bison bulls, cows, juveniles, and calves. A peak in diet quality occurred in May and June and followed a peak in C_3 production.

years of the study were combined before fecal nitrogen content was compared between groups. One peak in percentage fecal nitrogen occurred in May and June (Fig. 3), which suggests that there was an increase in diet quality at that time. This peak in consumption coincided with an observed peak in C_3 production (Tieszen et al. 1998). There was no apparent increase in quality of the diet concurrent with the observed increase in C_3 consumption or production noted in autumn.

We found no difference in fecal nitrogen between groups in June, December, January, and March (June, $F = 1.64$, $P = 0.196$; December, $F = 0.59$, $P = 0.63$; January, $F = 0.55$, $P = 0.65$; March, $F = 1.62$, $P = 0.22$). In April, percentage of fecal nitrogen was higher in calves and juveniles than cows and bulls ($F = 5.29$, $P = 0.0036$; Fig. 3). Percentage of fecal nitrogen in July differed between all groups and was highest in calves followed by juveniles, cows, and bulls ($F = 17.65$, $P = 0.0001$; Fig. 3). Fecal nitrogen in August was higher in calves than in any other group and higher in juveniles than in cows or bulls ($F = 6.42$, $P = 0.013$). Percentage of fecal nitrogen from bulls, cows, and juveniles in September was greater than from calves ($F = 7.76$, $P = 0.0004$). Percentage of fecal nitrogen from cows in October was greater than that of bulls, juveniles, and calves ($F = 7.01$, $P = 0.0009$).

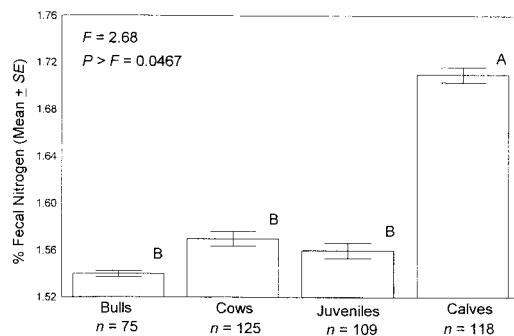


FIG. 4.—Fecal nitrogen summed over all months from April 1996 to December 1997. Bars with different letters indicate significant differences in percentage of fecal nitrogen between groups.

Percentage of fecal nitrogen from cows, juveniles, and calves in November was greater than from bulls ($F = 4.13$, $P = 0.0122$). When summed across years and months, percentage of fecal nitrogen from the calf group was greater than from other groups ($F = 2.68$, $P = 0.004$; Fig. 4).

DISCUSSION

Results of our research demonstrate that, with respect to $C_3:C_4$ ratio, the composition of the diets of all bison groups change as seasonal availability changes. Our data indicate 2 peaks of C_3 consumption for all groups studied. One peak occurs in the spring and 1 in autumn. This coincides with the observation of Vinton et al. (1993) that bison on the Konza Prairie Research Natural Area spent more time in spring and autumn in areas dominated by C_3 grasses and more time in summer in areas dominated by C_4 grasses. A similar pattern of change in diet composition was found for bison cows at 4 grassland sites in Oklahoma, Kansas, Nebraska, and North Dakota (Tieszen et al. 1998). Several studies have shown that C_3 grasses are higher in digestible dry matter than C_4 grasses (Hill et al. 1989; Wilson and Hacker 1987; Wilson and Hattersley 1989; Wilson et al. 1983). Thus, in periods when bison increase their consumption of C_3 grasses, nutrition in the

form of calories from soluble carbohydrates should increase as a result of an increase in dry matter digestibility of the diet.

Our results show that the overall diet quality of bison calves is better than that of bulls, cows, or juveniles. This result is not surprising given the fact that calves obtain nutrition from both nursing and grazing. Interestingly, the diets of calves are significantly better than other groups in July and August but worse in September. This reduction in the quality of calf diets coincides with the end of the breeding season for the Konza Prairie Research Natural Area herd. Green et al. (1993) noted that in the immediate postestrous period, calves of pregnant females experienced a significant decrease in nursing time and an increase in intervals between nursing bouts and increased their grazing time compared with calves of barren females. The average calving rate in the herd in 1994–1997 was 74.4% (Towne 1999). Thus, most calves in the herd should experience a decrease in maternal nutritional support in the postestrous period. Our data show that this decrease in maternal nutritional support results in a decrease in the diet quality of calves.

Across seasons, diets of juvenile bison usually did not differ in content or quality from that of cows. Juvenile bison are part of what is generally referred to as the cow-calf herd at the Konza Prairie Research Natural Area. Our observations of the herd suggest that from weaning to the onset of sexual maturity, juveniles spend a decreasing amount of time in close physical proximity to their mothers and an increasing amount of time in subgroups of peers that form within the larger herd. Thus, despite the fact that juvenile bison decrease the amount of time they spend in direct contact with their dams, they have access to the same quality forage as cows, and this is reflected in the similarity of their diets.

Our results do not provide support for the reproductive-strategy hypothesis, which predicts that males should use areas of

abundant and nutritious resources whereas females use areas that provide predictable resources and a safe site for offspring. Males in our study did not choose the most nutritious forage available. Further, bison cows appear to track resource quality on a seasonal basis and do not appear to be constrained in diet choice by the need to restrict foraging activity to areas that provide protection to offspring. Our findings are similar to those of Coppedge and Shaw (1998): Where recently burned areas contained relatively low biomass of grasses and presumably higher forage quality, bison cow-calf groups preferred recently burned areas, and bulls avoided recently burned areas.

Our study provides no support for the social-factors hypothesis, which makes no diet-specific predictions. Thus, it cannot explain why some groups might consume less than optimal diets, as our study shows bulls do. Although we did not make any direct measurements of habitat use by males and females, the many hours spent tracking the herd to collect fecal samples provided us with a good sense of group movements. Bulls and the cow-calf herd often were found in separate areas. However, it was not unusual to find both groups in the same area, particularly in spring and summer. When bulls and the cow-calf herd occupied the same area, they did so without apparent conflict. Based on our results and observations, we suggest that the social-factors hypothesis does not provide the best explanation for sexual segregation in bison.

Our results do provide support for the sexual dimorphism-body size hypothesis of sexual segregation in large ungulates. As this hypothesis predicts, male bison consume a lower-quality diet than do cows. Overall, diets of bulls contain a greater proportion of C₄ plants than do diets of the other groups we studied. Based on the observation that C₄ grasses are less digestible than C₃ grasses (Hill et al. 1989; Wilson et al. 1983; Wilson and Hacker 1987; Wilson and Hattersley 1989), this suggests that

bulls consume a diet that is lower in energy than the diets of cows, juveniles, and calves.

Bison bulls may adapt to the consumption of a lower-energy diet by consuming a greater amount of forage. Alternatively, if there are differences in the morphology or physiology of the digestive tracts of male bison compared with female bison, bulls may be able to extract more energy from equal amounts of forage than cows, juveniles, or calves. Further, despite the fact that they choose a different ratio of C₃:C₄ grasses, bulls do not experience a decrease in the quality of their diet compared with the quality of diets of cows and juveniles. Barboza and Bowyer (2000) developed a model based on gastrointestinal differences to explain sexual segregation in dimorphic deer. A similar model may apply to bison and explain why, despite the consumption of a less nutritious diet by bulls, diet quality does not differ between cows and bulls.

Ruckstuhl's (1998) foraging-behavior hypothesis has much in common with the body size-sexual dimorphism hypothesis. Both hypotheses invoke differences in body size as the causative factor in sexual segregation. The major difference in the 2 hypotheses is that the foraging-behavior hypothesis predicts evolution of sexual segregation in the absence of competition for food. The body size-sexual dimorphism hypothesis suggests that differences in digestive physiology allow males to use sites with high-fiber forage and thus reduce competition with cows for low-fiber forage. Because they are so similar in their foundation, assumptions, and predictions, our study provides support for the foraging-behavior hypothesis and the body size-sexual dimorphism hypothesis.

From an evolutionary standpoint, intersexual and intrasexual competition are the selective factors that lead to sexual dimorphism. As Ruckstuhl (1998) suggested, sexual dimorphism could lead to differences between sexes in factors such as bite size, rumen capacity, and step rate. Such mor-

phologic differences might then result in differences in foraging behavior and ultimately lead to segregation. Further, Ruckstuhl (1998) suggested that such segregation could take place in the absence of competition for food. We suggest that, for bison, sexual segregation could lead to an increase in reproductive success by reducing competition for limited low-fiber resources. If bison bulls have the capacity to extract more energy from a high-fiber diet than smaller females, then they are the group that would be expected to evolve a preference for the higher-fiber diet to reduce competition for a limited resource.

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