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Bighorn Sheep Diet Selection and Forage Quality in Central Idaho

Abstract

Rocky mountain bighorn sheep (*Ovis canadensis canadensis*) populations in the Big Creek drainage of central Idaho spend the winter on low elevation, southern exposures where snow depths are reduced or absent. Approximately 50% of the population migrates to higher elevations during warmer months, thus potentially extending the period of spring green-up and its accompanying higher levels of forage nutrient content and digestibility. Other bighorns remain on low elevation winter range year-round, experiencing warm, dry conditions and lower forage nutrient values earlier than sheep migrating to higher elevations. The objective of this study was to determine and interpret the seasonal diet selection of the non-migratory portion of the population. Microhistological analysis of composite fecal samples was used to determine diet composition, and plant samples were analyzed for crude protein, digestibility, and macro and micro nutrients to examine forage quality. Graminoids made up the majority of the diet throughout the year. During spring green-up when protein content and digestibility of grasses were at peak levels, consumption of forbs and browse declined. However, forbs and browse provided important sources of nutrients, especially protein, at critical times of the year when grasses were low in nutritional value and digestibility. Non-migratory bighorns had developed flexible and dynamic feeding behaviors that allowed them to meet their nutritional needs while remaining in a relatively warm, dry environment. Managers should focus on providing a diversity of plant species in all forage categories. Invasions of exotic plant species that reduce biodiversity may negatively impact bighorn sheep populations.

Introduction

Rocky Mountain bighorn sheep (Ovis canadensis *canadensis*) are regarded as specialized grazing animals adapted to a diet of coarse graminoid vegetation (Geist 1971). However, bighorns under some circumstances consume appreciable quantities of browse and forbs. In Colorado, summer diet of adult bighorn sheep consisted of 73-94% leaves of woody species, mainly true mountain mahogany (*Cercocarpus montanus*) (Rominger et al. 1988). The percentages of grasses, shrubs, and forbs reported in winter diets varied widely among populations. Shrubs comprised the highest percentage of forage in winter bighorn diets from Thompson Falls (Tilton and Willard 1981) and Sun River (Schallenberger 1965), Montana. Winter diets of bighorn sheep in British Columbia (Blood 1967), northcentral Montana (Kasworm et al.1984), and Yellowstone National Park (Oldemeyer et al. 1971, Keating 1985) were highest in graminoids. Hobbs et al. (1983) reported bighorn lambs selected a diet dominated by forbs, but later determined adult bighorns consumed mainly grasses (Baker and Hobbs 1987).

Studies that evaluated bighorn sheep diets throughout the year showed a variety of grasses, forbs, and shrubs were important at different times of the year. California bighorn sheep (*Ovis canadensis californiana*) in British Columbia depended on a diversity of forage alternatives (Wikeem and Pitt 1992). Similarly, desert bighorn sheep (*O. c. mexicana*) in Arizona consumed a wide variety of forage species throughout the year (Miller and Gaud 1989), and the authors concluded the dynamic nature of the desert environment required bighorns to adjust their diet in relation to changing vegetative conditions.

Hebert (1973) demonstrated that summer vegetation found at high elevation was on average more nutritious than similar vegetation found at lower elevations during summer, fall, and winter. In Hebert's study, captive bighorn sheep consuming high-elevation forages during the summer entered the winter in better physical condition, were more efficient at utilizing winter range forages, and responded faster physiologically to spring green-up than captive bighorns maintained on low elevation forages throughout the year. Essentially, bighorns "migrating" to higher elevations extended the period of consumption of nutritious spring forage, while bighorns consuming low elevation forage encountered senescent forage conditions months earlier.

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Within the greater Big Creek population approximately 50% of bighorn migrate over 60 km each spring from low elevation winter range to high elevation summer ranges, gaining over 1829 m in elevation (Smith 1954, Akenson and Akenson 1992). However, other bighorns do not migrate and remain on relatively dry, low elevation winter ranges throughout the year. The objective of this study was to determine and interpret seasonal diet selection of the non-migratory segment of the population from 1994 to 1997. We hypothesized non-migratory bighorns in Big Creek had developed flexible and dynamic feeding behaviors, similar to desert bighorn sheep, that allowed them to meet their nutritional needs while remaining in a relatively warm, dry habitat.

Study Area

Big Creek flows predominantly west to east and drains into the Middle Fork of the Salmon River (Figure 1). Elevations within the drainage range from 1067 to 2896 m, and southern exposures on the north side of Big Creek serve as important winter range to bighorn sheep, elk, and mule deer (*Odocoileus hemionus*). Snow depths are generally low and southern aspects usually remain snow-free for much of the winter. While winter range extends for 48 km along the lower portion of the

drainage, bighorn sheep occupy mainly the lower 19 km of the winter range.

Steep V-shaped canyons characterize topography at lower elevations, and abrupt changes in aspect result in markedly different plant associations. Soils are generally shallow and rocky, and numerous rock outcrops, cliffs, and talus slopes are present. Grasslands dominate southern exposures at lower elevations, where soil development is adequate.

Bluebunch wheatgrass (Pseudoroegnenia spicata). Idaho fescue (Festuca idahoensis), junegrass (Koeleria cristata), needle and thread grass (Hesperochloa comata), Sandberg's bluegrass (Poa sandbergii), and cheat grass (Bromus tectorum) are common species within grasslands. Grassland shrubs include big sagebrush (Artemesia tridentata), rabbitbrush (Erecameria nauseosa), and bitterbrush (Purshia tridentata). Curl-leaf mountain mahogany (Cercocarpus ledifolius) forms extensive stands on steep rocky outcrops, and arrowleaf balsamroot (Balsamorhiza sagittata), western yarrow (Achillea millefolium), and lupine (Lupinus spp.) are common forbs. Douglas-fir (Pseudotsuga menziesii) forests occur on north aspects and ridgetops, while small stands and individual Douglas-fir trees are scattered throughout the grasslands.

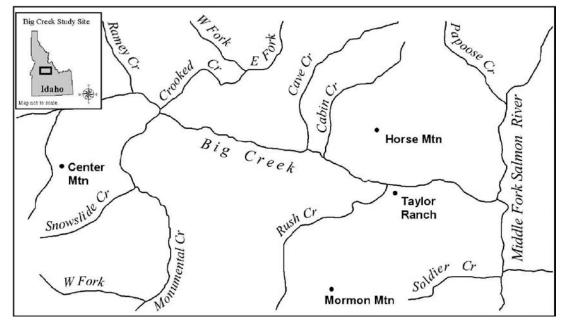


Figure 1. Big Creek winter range, Frank Church River of No Return Wilderness, Idaho.

Summers are typically hot and dry, with July and August usually having the highest average maximum temperatures. Maximum daily July and August temperatures averaged 29.8° C from 1994-1997 (National Weather Service 1994, 1995, 1996, 1997), and temperature patterns were relatively consistent from 1994 - 1997. However, September 1994 was unusually warm and dry, and produced average daily temperatures higher than those in August.

Moisture patterns were more variable than temperature patterns in the study area. Total annual precipitation during 1994-1997 was 31.3, 53.8, 39.4, and 43.1 cm (National Weather Service 1994, 1995, 1996, 1997). August and September are typically the months receiving the least precipitation. Most annual precipitation occurs during winter in the form of snow or as spring rain, with winter snowfall varying substantially between years. Snowfall from November - February totaled 37.3 cm during the winter of 1994-95, 93.7 cm during 1995-96, and 84.8 cm during 1996-97.

Bighorn sheep inhabiting the Big Creek drainage of central Idaho increased from approximately 70 individuals in 1973 to over 225 by 1991 (Akenson and Akenson 1992). The high population was associated with low lamb:ewe ratios, which averaged 12:100 from 1988 to 1991, compared to 46:100 from 1984 to 1987. Observations of small, sick lambs and the presence of several pneumoniacausing pathogens, including *Pasteurella trehalosi* and *P. multocida* (Hunter 1990, Jaworski 1993) suggested disease or intraspecific competition for food resources as possible explanations for low recruitment.

Methods

Diet Composition

Ungulate diet composition may be determined by: rumen analysis, microhistological fecal analysis, esophageal fistula, direct observation, or feeding site surveys (Litvaitis et al. 1994). In our study area, fecal analysis represented the best method for obtaining an estimate of diet composition for free-ranging bighorn sheep (Todd and Hansen 1973, McInnis et al. 1983, McInnis and Vavra 1987, Wikeem and Pitt 1992). Fecal analysis enabled us to follow the seasonal diet selection of a group of animals through time without eliminating or capturing individuals. While the results of fecal analyses may be influenced by differential digestibility, they have produced acceptable results for determining bighorn sheep diets (Todd and Hansen 1973). Direct observations of feeding on identifiable plant species were possible; however, such observations did not occur with sufficient frequency to reliably estimate diet composition. Informal feeding site examinations were conducted to obtain a general knowledge of utilized plant species and parts, but were not included in formal analysis because sites were sometimes occupied by elk and mule deer, as well as bighorn sheep.

Pellet samples were collected between June 1994 and February 1995, January and August 1996, and January and May 1997. Since mule deer shared winter and summer ranges with bighorns, and their pellets are similar in appearance to bighorn sheep pellets, only pellet groups directly observed from bighorn sheep were collected. Mature rams accompanied ewes from late fall to early spring, and immature rams remained with ewe bands through the summer months. Consequently, fecal samples contained pellets from adult, yearlings, and lambs of both sexes. Six pellets were collected from multiple fecal piles after sheep had left bedding areas, feeding sites, and mineral licks.

Microbial decomposition of pellet samples was prevented by adding an equal volume of table salt and air-drying in paper bags (Hansen et al. 1978). Analyses were conducted on composite samples formed by combining pellets collected during two week increments of the study period. Composite samples were analyzed at the Washington State University Wildlife Habitat Laboratory in Pullman, Washington, and each composite sample received 150 microscope views. Forage species were identified to the lowest taxon possible, and the percentage each forage species contributed to a composite fecal sample determined.

Forage Quality

Composite samples of known forage species were collected for nutritional analysis from sites where bighorns were frequently observed feeding. A compass bearing was randomly generated on a hand-held calculator, and a portion of the species being sampled was collected from the nearest plant at approximately five-meter intervals, with at least ten plants sampled at each site. Each forage species was collected from three different sites at approximately two-week intervals. The species collected were determined from direct observation (Wagner 2000) and from a previous diet study conducted in the area (Smith 1954). Samples were placed in paper bags, air-dried, then oven dried at 40° C for 48 hr. Plant parts known to be consumed by bighorn sheep (Smith 1954, Wagner 2000) were separated and ground with a Wiley mill to pass through a 1 mm screen. For example, bighorns consumed leaves, current annual growth, and smaller twigs of shrub species, and these parts were separated from large woody stems before grinding.

Portions of composite samples were analyzed at the University of Idaho Analytical Sciences Laboratory in Moscow, Idaho for macro-(sodium, potassium, calcium, magnesium, phosphorus, and sulfur) and micro-(chromium, cobalt, copper, iron, manganese, and zinc) minerals, by inductively coupled plasma optical emission spectroscopy (ICP) (Anderson 1996). Total carbon, hydrogen, and nitrogen were determined by furnace combustion, and crude protein was estimated by multiplying total N by 6.25 (Robbins 1993). The study site occurs in an area of low selenium, and selenium deficiencies may occur in ungulates (Robbins 1993). Therefore, a separate analysis for selenium was conducted on a subset of composite samples for bluebunch wheatgrass, curl-leaf mountain mahogany, and bitterbrush. Selenium was analyzed by ICP after the sample was first treated by acid digestion using nitric, perchloric, and sulfuric acids, followed by hydride generation before being subjected to ICP (Anderson 1996, Tracy and Moller 1990). This pre-treatment helps free selenium bound within cell wall matrices, thus providing a more accurate determination of selenium content.

Apparent *in vitro* digestible dry matter (IVDDM) was determined using a modified version of the method developed by Tilley and Terry (1963). Forage samples of 0.25 g were placed in porous bags, heat sealed, and incubated in an Ankom Technology Daisy II 200/220 Rumen Fermenter for 48 hr at 39 °C. Inoculum was obtained from three domestic beef cows maintained on a grass diet. Two replicate trials were conducted and the values averaged. The residue obtained after fermentation was a combination of undigested substrate and microbial cells (Van Soest 1982). Correction factors to subtract the microbial cell fraction adhering to bags within each batch of

inoculum. Correction factors were applied by averaging dried weights of blanks and subtracting this value from sample weights.

Data Analysis

Based on annual reproductive cycles of bighorn ewes and plant phenology, we divided the year into 5 seasons (Table 1). Summer (1 June to 16 August) corresponded to peak lamb drop, lactation, and availability of early summer forage. Late summer-fall (17 August to 15 November) corresponded to decreased lactation, gradual senescence of most herbaceous forage, possible fall resprouting of certain grass species following rains, and onset of cold, moist weather. Winter (16 November to 15 February) corresponded to frequent snowfall, relatively low temperatures, senescent forage, and mating. Late winter (16 February to 31 March) corresponded approximately to the second trimester of gestation and earliest green-up of certain grasses. Spring (1 April to 31 May) corresponded to the third trimester of gestation, green-up of all forages, and eventually movement of ewes to lambing areas.

Percent diet compositions of forage species were calculated by averaging the values from individual composite fecal sample values within season. Only forage species with $\geq 1\%$ diet composition for at least one season were included in analyses. Forage species were also categorized as grasses, forbs, browse, conifers, and mosses/lichens, and percent diet composition was calculated for each category. Differences in the annual use of forage categories were examined by combining seasons and comparing the percent composition of forage categories among years using a t-test or one-way analysis of variance (ANOVA). Differences in forage use among seasons for grass, forb, and browse categories were evaluated with a one-way multivariate analysis of variance (MANOVA) followed by univariate ANOVA. Means were separated using Duncan's multiple range tests. Diet composition percentages were treated as normally distributed and were not arcsine transformed, as transformation did not alter estimates of the variance beyond the third decimal place, and consequently did not affect the results of statistical tests (Hobbs et al. 1981). In addition, Butchner and Kemp (1974) found no difference in statistical power between analysis of variance using transformed and non-transformed data. When sample sizes differed, random subsampling was conducted to obtain balanced designs that were more robust to violations of the assumption of heterogeneity of variance (Kirk 1982).

Seasonal trends in crude protein, IVDDM, and macro and micronutrients were analyzed by linear and polynomial regression.

Results

Diet Composition

Pellets were collected from 999 fecal piles, which were separated into 40 composite samples for laboratory analysis. Eight composite samples were analyzed for summer, late summer-fall, late winter, and spring. Fourteen composite samples were analyzed for winter. The number of fecal piles from which pellets were collected varied, and depended upon the group size and its behavior. Large numbers of fecal piles were easily located where sheep concentrated and were sedentary, such as bedding sites and mineral licks. At feeding sites, fecal piles were dispersed and more difficult to locate. Pellets were obtained from approximately 70 individual sheep; however, the number of sheep on the study area fluctuated, with more sheep being present during winter.

Browse constituted a significantly higher proportion of the diet (P = 0.001) in 1995-96 than in 1994-95 or 1996-97. Shrubs comprised 37.27% of fecal samples during 1995-96 compared to 3.04% and 10.45% in 1994-95 and 1996-97.

Based on MANOVA, percent diet composition of grasses, forbs, and browse differed among seasons (P = 0.001). Univariate tests indicated significant differences (P = 0.001) in seasonal use of grasses, forbs, browse, conifers, and mosses. Partial correlation coefficients showed grass consumption was inversely related to both forb and browse consumption (-0.84 and -0.68).

Graminoids formed the largest component of bighorn diet during all seasons (Figure 2), and bluebunch wheatgrass formed the largest singlespecies component of the diet in all seasons (Table 1). Idaho fescue, bluegrasses (*Poa* sp.), and needleand-thread grass were important during all seasons, but reached their peak in percent diet composition

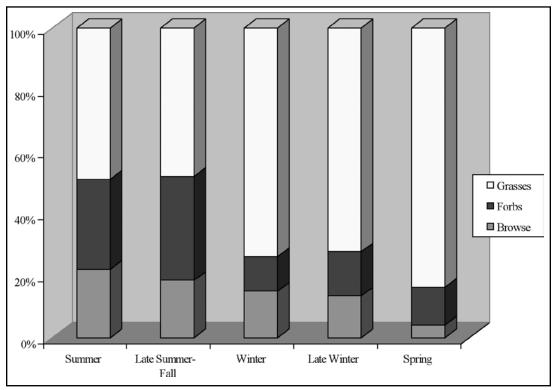


Figure 2. Percent diet composition of grasses, forbs, and browse in the diet of bighorn sheep from the Big Creek drainage of central Idaho, as determined from fecal samples collected from 1994 to 1997.

Species	Summer 1 June-15 Aug.	Late Summer Fall 16 Aug15 Nov.	Winter 16 Nov15 Feb.	Late Winter 16 Feb31 March	Spring 1 April-31 May
Graminoids	48.4	48.0	73.8	66.0	79.9
Bluebunch wheatgrass	14.9	23.3	33.0	23.6	22.2
Pseudoroegnenia spicata					
Cheatgrass	5.5	2.2	3.4	1.8	2.4
Bromus tectorum					
Brome	1.2	0.0	1.1	4.4	4.1
Bromus sp.					
Idaho fescue	6.6	3.0	6.2	7.0	12.4
Festuca idahoensis					
Junegrass	1.1	2.3	2.5	0.8	1.6
Koleria cristata					
Bluegrass	8.8	7.4	10.5	9.8	14.4
Poa sp.					
Squirreltail grass	0.0	0.0	0.7	1.1	0.7
Sitanion hystrix					
Needle-and-thread grass	7.3	8.2	14.8	14.5	16.9
Hesperochloa comata					
Forbs	28.7	33.5	11.3	13.0	11.6
Yarrow	3.1	2.4	0.4	0.3	0.5
Achillea millefolium					
Rockcress/Thelypody	1.7	8.1	0.6	0.6	0.5
Arabis/Thelypodium					
Milk vetch	1.9	1.8	0.2	0.3	0.3
Astragalus sp					
Arrowleaved balsamroot	0.5	0.2	3.4	6.6	4.7
Balsamorhiza sagittata					
Thistle	2.3	0.5	0.4	0.2	0.2
Cirisium sp.					
Tansymustard	0.1	1.0	0.0	0.0	0.2
Descurainia pinnata					
Willow-weed	0.8	1.1	0.0	0.0	0.0
Epilobium sp.					
Horsetail	1.2	0.1	0.0	0.0	0.0
Equisetum sp					
Fleabane	0.4	2.4	0.0	0.1	0.2
Erigeron sp.					
Buckwheat	0.7	1.8	0.3	1.3	0.7
Eriogonum sp.					
Bladderpod	0.4	6.4	0.3	0.0	0.1
Lesquerella sp.					
Lupine	0.7	2.1	0.6	0.7	0.9
Lupinus sp.					
Penstemon.	1.3	0.9	0.2	0.1	0.0
Penstemon sp.					
Phacelia	2.7	0.1	1.0	0.3	0.3
Phacelia sp.					
Other forbs	3.3	3.1	1.0	1.5	1.4
Browse	21.9	18.4	14.9	12.3	3.9
Serviceberry	0.0	1.1	0.3	0.4	0.2
Amelanchier alnifolia					
Oregon grape	0.4	2.1	0.9	1.6	0.5
Berberis repens					

TABLE 1. Average seasonal composition of plant species (≥ 1%) in bighorn sheep diet from Big Creek, Idaho 1994-1997, as determined by microhistological fecal analysis.

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Species	Summer 1 June-15 Aug.	Late Summer Fall 16 Aug15 Nov.	Winter 16 Nov15 Feb.	Late Winter 16 Feb31 March	Spring 1 April-31 May
Mountain-mahogany	6.1	0.2	6.1	6.1	1.1
Cercocarpus ledifolius					
Ninebark	2.8	1.2	0.1	0.2	0.5
Physocarpus malvaceus					
Bitter-brush	6.8	9.1	4.3	1.4	0.7
Purshia tridentata					
Currant	1.9	0.0	0.1	0.0	0.1
Ribes sp.					
Willow	0.6	0.8	0.7	1.8	0.1
Salix sp.					
Conifer	0.3	0.0	1.4	8.1	3.4
Douglas-fir	0.0	0.0	1.0	7.3	3.2
Pseudotsuga menziesii					
Moss	0.0	0.0	0.1	1.1	0.9

TABLE 1. Average seasonal composition of plant species (≥ 1%) in bighorn sheep diet from Big Creek, Idaho 1994-1997, as determined by microhistological fecal analysis.

during spring. Highest consumption of grasses occurred during winter and spring (Figure 2), and lowest consumption occurred during summer and late summer-fall (P = 0.001).

Forb consumption peaked in summer and late summer-fall (Figure 2). Significantly more forbs were consumed during these 2 seasons than during winter, late winter, and spring (P = 0.001). The most prominent dietary species were western yarrow, thelypody (Thelypodium sp.), milk vetch (Astragalus sp.), thistle (Cirisium sp.), buckwheat (Eriogonum sp.), bladderpod (Lesquerella sp.), Lupine, and Phacelia (Phacelia sp.) (Table1). As expected, forbs formed a much smaller proportion of the diet in winter due to senescence. Arrowleaf balsamroot was a major exception, reaching peak levels in the diet during winter months. Bighorn frequently pawed through snow to consume semidecomposed balsamroot leaves. Buckwheat sp. and Phacelia sp. also persisted in the diet during winter months. Biscuitroot (Lomatium dissectum) was not identified in the microhistological fecal analysis. However, during the winter, bighorn sheep were often observed pawing up and consuming tubers of this plant whenever the ground was not frozen. Bighorns also consumed arrowleaf balsamroot tubers, and biscuitroot tuber fragments appear identical to arrowleaf balsamroot fragments under the microscope (Kasworm et al. 1984). Therefore, the presence of biscuitroot in the diet may have been overlooked in the microhistological fecal analysis.

Browse consumption was greatest during summer and late summer-fall (Figure 2, Table 1), declined in winter and late winter, and fell to lowest levels during spring. Significantly more browse was consumed during summer, late summerfall, and winter, than during spring (P = 0.001). However, during the winter of 1995-96, browse consumption was significantly higher compared to other winters during this study. The major browse species consumed were mountain mahogany and bitterbrush (Table 1). However, ninebark (Physocarpus malvaceus), currants (Ribes sp.), and serviceberry (Amelanchier alnifolia) were of importance during summer and late summer-fall, and willows (Salix sp.) were important during late winter. During late summer-fall, bighorn sheep were observed feeding on elderberry (Sambucus cerulea), but this species did not exceed 1% diet composition. Conifers, mainly Douglas-fir, appeared in the diet during winter, late winter, and spring (Table 1). Only twice during the study were bighorns observed browsing on Douglas-fir. However, Douglas-fir needles were often mixed with Idaho fescue on the ground. Therefore, some needles may have been consumed while sheep were grazing beneath trees during winter.

Forage Quality

Protein content of grasses and forbs was highest during spring, and declined throughout summer and late summer-fall to lowest levels in winter (Figures 3 and 4). By late-winter, crude protein

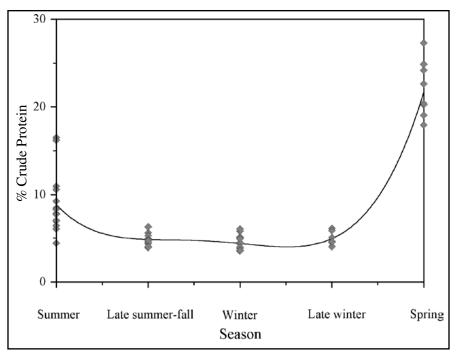


Figure 3. Polynomial regression of percent crude protein (CP) on season for grasses collected from the Big Creek drainage of central Idaho from 1994 to 1997, $CP = 36.4-50.5x + 29.9x^2-7.8x^3+0.7x^4$, N = 56, $R^2 = 0.90$.

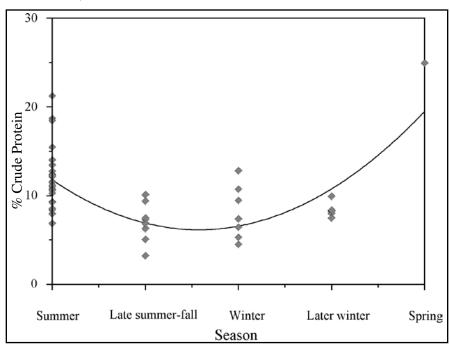


Figure 4. Polynomial regression of percent crude protein (CP) on season for forbs collected from the Big Creek drainage of central Idaho from 1994 to 1997, $CP = 21.2-11.7x + 2.3x^2$, N = 51, $R^2 = 0.42$.

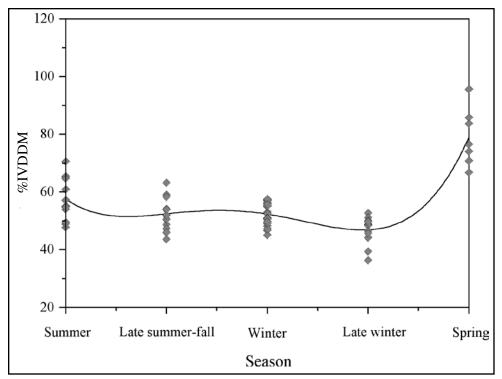


Figure 5. Polynomial regression of percent in vitro digestible dry matter (IVDDM) on season for grasses collected from the Big Creek drainage of central Idaho from 1994 to 1997, IVDDM = $131.3-142.4x+90.4x^2-23.9x^3+2.2x^4$, N = 67, $R^2 = 0.71$.

levels slowly increased, and rapidly reached peak levels during spring. Crude protein levels of grasses and forbs were not significantly different during spring or summer, but forbs contained significantly more protein than grasses through late summerfall, winter, and late winter (P = 0.001). Protein content of shrubs remained relatively constant through all seasons.

IVDDN of grasses decreased from spring through late summer-fall, reaching its lowest level during late winter before rapidly increasing during spring (Figure 5). For forbs and browse, IVDDM did not show significant seasonal relationships, but tended to follow patterns similar to grasses.

Phosphorus, potassium, and sulfur content of grasses, forbs, and browse followed a seasonal pattern similar to crude protein, with high levels during summer, declining steadily to low levels during winter, and rapidly increasing during spring. Magnesium content of grasses and forbs followed this pattern; however no such relationship existed for browse. Copper followed the same relationship for grasses and shrubs, but no relationship existed for forbs. Zinc content of grasses demonstrated a quadratic relationship, with highest content during summer and spring green-up. No relationship between zinc content and season was evident for forbs and shrubs.

Calcium content in grasses and forbs maintained a roughly constant level throughout the year, therefore, the calcium-phosphorous ratio increased during late summer-fall and winter months. Sodium content did not exhibit any significant trends through time for grasses, forbs or shrubs. Trends in iron content were erratic for all three forage categories. Few samples from any forage category contained detectable levels of the trace minerals cobalt, chromium, and selenium.

Discussion

Bighorn sheep inhabiting lower elevations of Big Creek drainage conform to Geist's (1971) assertion that bighorns are primarily grazing animals. However, during certain seasons forbs and shrubs are important components of sheep diets in this drainage. Seasonal differences in diet are largely associated with changing proportions of forb and shrub consumption. Daily et al. (1984) in Colorado and Wikeem and Pitt (1992) in British Columbia reported similar high forb consumption patterns during warmer seasons, followed by reductions in consumption with the senescence of forbs.

Forbs may collectively furnish an important source of nutrients during peak lactation, and enable bighorns to accumulate nutrient reserves prior to winter. During summer and late summerfall the average crude protein content of forbs was higher than grasses, and certain individual forb species had much higher crude protein content than grass species. For example, thelypody averaged 16.3% crude protein content, while bluebunch wheatgrass averaged 4.8% during late summer-fall (Table 1). For grazing ruminants, the minimum dietary protein requirement is approximately 4.5% (Robbins 1993). Even though both forage categories were declining in protein content and other nutrients, nutrient content of forbs did not decline as rapidly as grasses.

Most forbs reached senescence by winter, and were covered by snow. Therefore, their general decrease in diet frequency was expected. Forbs that persisted in the diet (Table 1) were made available by pawing through snow or gravel (arrowleaf balsamroot leaves and tubers and biscuitroot tubers), persisted with a woody base (*Eriogonum* sp.), or grew along talus slope margins (*Phacelia* sp.). These forbs maintained crude protein and IVDDM values above grasses during winter.

Shrubs were most heavily consumed during summer and late summer-fall. The most common dietary shrub was curl-leaf mountain mahogany, which grows primarily on steep rock outcrops and cliffs. Bighorn ewes lambing at low elevations select such sites to reduce predation risks (Festa-Bianchet 1988). This behavior places ewes close to mountain mahogany during summer when new growth is available. In contrast to our results, Smith (1954) reported summer as the period of lowest shrub consumption, but he included bighorns living at higher elevations in his study, where mountain mahogany is less common.

During late summer-fall, crude protein content of grasses at lower elevations was declining, while average crude protein content of shrubs remained nearly constant. Crude protein content of curl-leaf mountain mahogany parts consumed by bighorn ewes averaged 12% during summer and late summer-fall, a period during which crude protein content of grasses had declined to 5%. While the presence of tannins reduces protein availability in some shrub species (Robbins et al. 1987), Cook (1990) reported only trace amounts of tannins in true mountain mahogany in Wyoming.

Shrub consumption during winter, when perennial bunch grasses are lowest in crude protein and IVDDM, may prevent bighorn sheep from entering a negative protein or energy balance. Shrubs contributed the greatest proportion to the diet during winter along the Clark Fork River in Montana (Tilton and Willard 1981) and Wikeem and Pitt (1992) reported bighorns in British Columbia browsed most during winter. In central Idaho, Smith (1954) observed bighorns consuming greater amounts of browse during winter months. Browse may become important when large areas of winter range are periodically covered by sheet ice preventing bighorns from grazing (Smith 1954). During such occurrences bighorns may move to cliffs to browse on shrubs or grasses growing next to large heat-absorbing rock outcrops.

Grasses increased to high dietary levels during winter, and were also reported to be the major winter forage category by Smith (1954), Blood (1967), Oldemeyer et al. (1971), Dailey et al. (1984), Kasworm et al. (1984), Keating et al. 1985, and Wikeem and Pitt (1992). Bluebunch wheatgrass was the most utilized forage species in all seasons. Bluebunch wheatgrass peaked in diet frequency during January and Februarv in bighorn diet in British Columbia, where bluebunch wheatgrass culms protruded above the snow, remaining more visible and available than other grasses (Wikeem and Pitt 1992). We also observed increased feeding upon bluebunch wheatgrass during and immediately following snowfall. Bighorns frequently foraged on Idaho fescue beneath Douglas-fir canopies, possibly because of reduced snow pack in those areas. Bluegrasses and needle-and-thread grass were among the first plants to initiate green-up, and often exhibited green growth during the latter weeks of winter on southern exposures or near sources of heat, such as rock outcrops. Bighorns quickly used these species, possibly because crude protein content of new growth was considerably higher than senescent bluegrass material.

During spring green-up, shrub diet frequency dropped to its lowest levels, while grass diet frequency peaked as reported by Smith (1954). This corresponded to peak crude protein and IVDDM levels of grasses on the study area. During other time periods when grasses were lower in crude protein, bighorn may have consumed shrubs to obtain protein in spite of potentially higher lignin levels. Baker and Hobbs (1987) reported that increased shrub consumption resulted in increased mean retention times in the rumen for grasses and browse. However, protein obtained from shrubs may maintain a healthy rumen environment for microbes when grasses are low in crude protein.

The abundant nutrients found in grasses during spring appear at a critical time for adult ewes. Fetal growth follows a non-linear trajectory with the greatest growth occurring during the latter stages of gestation, and parturition is soon followed by the even more demanding nutrient requirements of lactation (Robbins 1993). These events in the life of an adult ewe correspond to the period of abundant nutrients found in grasses during spring and the earlier months of summer.

Certain elements, such as sulfur, are chemical constituents of amino acids, and several elements, such as phosphorous, potassium, sulfur, magnesium, copper, and zinc, generally followed an annual cycle of abundance similar to crude protein levels in grasses. For the proper absorption and metabolism of calcium and phosphorus, calcium to phosphorous ratios should range from 1:1 to 2:1 (Robbins 1993). Phosphorous levels may decrease to low levels over winter while calcium levels remain relatively stable, thus producing a high ratio (Demarchi 1968), and our results were similar. Excesses of calcium do not affect phosphorous absorption as much as phosphorous excesses affect calcium absorption (Robbins 1993).

In contrast to domestic sheep, nutrient requirements for macro and micro minerals have not been experimentally determined for bighorn sheep. Robbins (1993) argued wild animals have faced entirely different selection pressures from those of domestic animals, and consequently would not be expected to have similar nutrient requirements. Therefore, it is difficult to evaluate whether bighorn sheep in Big Creek suffered from a lack of these nutrients by using data available for domestic sheep. However, the data presented here identified mid- to late-winter and early spring as the seasons when bighorn sheep would most likely experience nutrient deficiency. Certain trace elements, such as selenium, chromium, and cobalt, occurred in amounts below detectable limits or were present in very small quantities in the forage samples analyzed. These data suggest that these important micro-nutrients may be deficient in the diet of bighorn sheep in Big Creek.

We found non-migratory bighorn sheep inhabiting the lower elevations of Big Creek had developed flexible and dynamic feeding behaviors that allowed them to adapt to changing plant phenologies and accompanying variations in plant nutritional content. Although grasses make up the majority of plants consumed, forbs and shrubs furnished high quality nutrients at key times during the year. Various forb and grass species reached senescence at different times of the year, and plant species displayed a wide range of nutrient content through the yearly cycle. Shrubs offered a more consistent source of nutrients, but with higher lignin content. A diverse plant community provided bighorn sheep the opportunity to vary diet composition through the seasons.

Management Implications

Bighorn sheep (*Ovis canadensis canadensis*) in the Northern Rocky Mountains have generally offered biologists greater management challenges than other North American ruminants (Cook 1990). Bighorn sheep populations have suffered from a general loss of habitat and disease outbreaks throughout their range (Risenhoover et al. 1988). Protection, either through relatively strict hunting regulations or total hunting closures, has generally failed to promote recovery of bighorn sheep populations with the same degree of success witnessed for other native ruminants, such as white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*).

A less diverse plant community may compromise the ability of bighorn sheep to adapt to a changing environment. Exotic weeds such as spotted knapweed (*Centaurea maculosa*) have invaded the Big Creek winter range. Such exotic invasions may result in a decrease in plant species diversity (Whitson et al. 1996). If low-elevation bighorn herds rely on a diverse plant community to meet their nutritional needs, then these exotic invaders may pose a threat to future generations of bighorn sheep. It is important for land managers to provide a diverse plant community for bighorn sheep, and this may require the control of exotic plant species in wilderness areas.

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