

**UNIQUE ASPECTS OF THE ECOLOGY OF BIGHORN SHEEP OCCUPYING A
CLAY HILLS-PRAIRIE ENVIRONMENT IN BADLANDS NATIONAL PARK**

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Abstract: Bighorn sheep (*Ovis canadensis*) numbers throughout western North America declined dramatically during the late 1800's and early 1900's (Seton 1927, Cowan 1940). Nearly a century after experiencing catastrophic losses, many bighorn populations have yet to recover to historical levels (Hoefs, 1984). Restoration and maintenance of viable populations is the primary goal of bighorn sheep management. This paper investigates the incidence of lungworm disease, effects of fire on forage quality; dietary content; and habitat selection by bighorn sheep that occupy a clay hills-prairie environment in Badlands National Park, South Dakota. Bighorn sheep herds in the north and south units of Badlands National Park differ in their founding history, total population and population density. The incidence of lungworm larvae in

bighorn sheep fecal samples were higher in the north unit. Infestation levels were unrelated to variation in yearly rainfall totals. For five forage plant species, only minor changes in dry weight, percent nitrogen, percent protein, and dry matter digestibility were detected in the two years following seasonal burn treatments. Microhistological analysis of fecal samples indicated that *Agropyron spp.* were the dominant forage in the ^NNorth ^Uunit and *Stipa spp.* were dominant in the ^SSouth ^Uunit. Seasonal habitat use data showed that ewe groups were most often observed on elevated sod buttes during the winter and spring; on shadier midslopes and ridges during the summer; on or near the steepest escape terrain during lambing; and farthest from escape terrain during the rut.

INTRODUCTION

Historically, bighorn sheep (*Ovis canadensis*) occupied larger geographic ranges than they do now (Buechner 1960, Geist 1971). Population levels of bighorn sheep declined dramatically throughout western North America during the late 1800s and early 1900s (Seton 1927, Cowan 1940). Bighorn sheep are influenced by many factors including habitat quality, population density, weather, and disease. While unregulated market hunting, habitat loss to domestic grazing, and human development contributed to the demise, various virulent diseases are suspected to have played the key role in historic declines (Seton 1927, Cowan 1940, Risenhoover et al. 1988, Smith et al. 1991). Some combination of factors continue to limit the abundance of wild sheep. Nearly a century after experiencing catastrophic losses,

many bighorn populations have yet to recover to historical levels (Hoefs, 1985).

Among areas where sheep have been extirpated are the western Great Plains. The Audubon's subspecies that occupied the Badlands area (*O. c. auduboni*) were eradicated earlierⁱⁿ the 1920's. Recent efforts have reintroduced bighorn sheep from the Rocky Mountains into some of the Audubon's bighorn sheep's historic range within Badlands National Park (Benzon 1990).

In 1964, 22 Rocky Mountain bighorns from Pikes Peak, Colorado were placed within an enclosure inside Badlands National Park. Following a disease die-off attributed to *Pasteurella*, the 14 surviving bighorn sheep were released from the enclosure into the north unit of the park in 1967. The herd grew very slowly and still numbered only 27 in 1980 (McCutcheon 1980). The herd subsequently increased and, by 1990, 93 bighorn sheep were reported by observers. During the 1980's, sporadic observations of dispersing bighorn sheep occurred in the ^South ^Unit. In 1991, an aerial survey confirmed the presence of 30 Rocky Mountain bighorn sheep in the ^South ^Unit, in a locale centered over forty kilometers to the southwest of the ^North ^Unit.

Data from five census flights flown between September 1992 and October 1994 were corrected for sightability bias with Aerial Survey software (Unsworth et al. 1994). Estimates indicate a population of 120 sheep in the north unit and 45 sheep in the south unit in 1994. Based on the amount of habitat area available to bighorn sheep (Sweanor et al. 1995), estimates of bighorn sheep densities are substantially higher in the ^North ^Unit than in the ^South ^Unit (0.86 sheep/km^2 and 0.17 sheep/km^2 , respectively). A lamb:ewe ratio of 42:100 for the entire park population estimated

from the October 1994 census flight suggests a stable or slightly increasing population trend (Singer et al. 1995).

To monitor and manage the bighorn sheep population in Badlands National park, a research plan was developed to address the following objectives: 1) quantify current levels of lungworm larvae occurrence in bighorn sheep fecal samples as a baseline condition for future monitoring, 2) determine bighorn sheep dietary components, 3) analyze the possible use of different seasonal fires to improve grazing habitat for bighorns, and 4) determine bighorn ewe seasonal habitat preferences. Bighorn sheep herds in the ^North and ^South ^Units of Badlands National Park differ in their founding history, total population and population density. We hypothesized that: 1) the incidence of lungworm larvae incidence in the south unit would be lower due to the lower population density, 2) bighorn dietary content in the two units would differ due to inherent variations in plant availabilities and would reflect a greater opportunity for sheep in the lower-density south unit to demonstrate preference, 3) fires in the mixed grass prairie habitat would have a positive effect on grassland biomass and quality, and 4) habitat use by ewe groups in the ^North ^Unit would vary by season.

Lungworm Larvae Incidence

Infectious and parasitic diseases pose significant obstacles to successfully restoring and managing populations of bighorn sheep. Protection from disease will be an integral part of the successful management and expansion of existing

populations (Singer et al. 1993).

The level of disease induced mortality in the Badlands National Park herd has never been thoroughly evaluated. In February of 1992, 20 Rocky Mountain bighorns were captured in the north unit and 7 in the south unit (Singer et al. 1993). Both herds were examined and found to be infected with lungworms (*Protostrongylus stilesi* and *P. rushi*). Annual fluctuations in snail numbers may affect infection rates in bighorns. Snails may be more abundant in moist conditions. Areas in Montana with the most severe lungworm infections in bighorns also had the highest densities of snails (Forrester and Senger 1964).

Diet Selection

Herbivore diet selection may directly influence ecosystem structure (Ellis et al. 1976). Selective feeding behavior may be influenced by a number of factors including forage availability (Hobbs and Swift 1988) and population density (McNaughton 1979). Fecal analysis has proven useful in estimating seasonal diets (Hansen and Dearden 1975, Hansen and Reid 1975) and evaluating diets based on spatial location (Hansen and Clark 1977, Hansen et al. 1977).

Effects of Fire on Forage Quality

Large and frequent fires were part of the historic setting of the mixed grass prairie, including what is now Badlands National Park. Fires in the mixed-grass

prairie increased biomass of forages (Kelting 1957, Adams et al. 1982, Peet et al. 1975, Rice and Parenti 1978), increased flowering of grasses (Peet et al. 1975), and increased the relative proportion of forbs (Daubenmire 1968). Responses of bighorn sheep to burning has been extensively studied in Rocky Mountain environments, but to a much less degree in a prairie environment. Bighorn sheep populations benefit from burning in most forested situations. Bighorn foraging efficiency is greater (Hurley and Irwin 1986), their diet quality is higher (Hobbs and Spowart 1984), their horns grow faster and their lungworm infestation rate is lower (Seip and Bunnell 1985) on burned ranges. Forages on burned bighorn ranges greened up earlier and greenup lasted longer, in some instances through the entire first winter following spring burning (Hobbs and Spowart 1984). Similar information, however, does not exist for bighorns occupying mixed grass prairie badlands habitat.

Evidence of benefits from both spring and fall burning can be found in the literature. Spring burning is felt to enhance grasslands more than fall burning since the time to growth initiation is less (Anderson 1965, Owensby and Anderson 1967). However, other studies suggest greater enhancement from fall burning, or no difference (James 1985). Burning just prior to a drought period can result in poor results from burning, regardless of the season of burning. Prescribed fire is one of the few active management measures that park staff could take to benefit bighorn sheep. Fire suppression may have resulted in unnatural conditions on bighorn ranges. Burning may reduce lungworm rates and increase the area used by bighorns.

Habitat Selection

Most habitat studies of bighorn sheep have occurred in mountainous environments (Buechner 1960; Geist 1971; Risenhoover and Bailey 1985; Tilton and Willard 1982; Cook 1990) and have made some reference to seasonal habitat associations. Habitat characteristics such as slope, aspect, distance to escape terrain, and vegetation types have been recognized as important features of mountainous sheep environments (Geist 1971; Risenhoover and Bailey 1985; Cook 1990). Few studies have involved low-elevation non-mountainous prairie regions (Fairbanks, Bailey and Cook 1987). Badlands National Park presents a unique opportunity to study seasonal habitat characteristics of a self-sustaining low-elevation non-mountainous prairie bighorn sheep herd.

STUDY AREA

Badlands National Park is located in southwest South Dakota. Surrounded by gently rolling grassland, the rugged landscape varies in elevation from 850 m to 1025 m., to form steep canyons, exposed ridges, pinnacles, and buttes. Erosive influences from the White river near the park's southern boundary resulted in the diverse park topography (Thornbury 1965). Mixed-grass prairie occurs on the upland plateau and lower grasslands, as well as on the tops of buttes and lower sod-covered slumps. Annual precipitation averages 40 cm. Summer temperatures may exceed 38° C and winter temperatures may drop below -18° C.

The park's flora is characterized by mixed-grass prairie found on the lowlands, tables, and tops of buttes. Many grass species such as blue grama (*Bouteloua gracilis*), green needlegrass (*Stipa viridula*), western wheatgrass (*Agropyron smithii*), and porcupine grass (*Stipa comata*) occur. Shrubs and herbaceous plants such as silver sage (*Artemisia ludoviciana*), rubber rabbitbrush (*Chrysothamnus nauseosus*), prickly pear (*Opuntia polyacantha*), and scarlet globemallow (*Sphaeralcea coccinea*) are found. Trees, such as cottonwood (*Populus deltoides*) occur along riparian areas. Rocky mountain juniper (*Juniperus scopulorum*) is often found in groves on the southern exposures of buttes and scattered within ravines.

METHODS

Incidence of Lungworm Larvae

Fresh bighorn sheep fecal piles were collected by field personnel from the June 1992 through the August 1993. The Baermann technique was used to determine the number of first-stage larvae per gram (LPG) of dry feces. A multi-response permutation procedure (MRPP, Biondini 1988 and Mielke 1991) was used to compare the following: levels of lungworm larvae incidence in the North and South Unit samples; presence or absence of lungworm larvae in North and South Unit samples; and levels of lungworm larvae incidence in different seasons in North Unit samples. Annual data on lungworm infection levels was used to test for relationship to annual precipitation.

Diet Selection

Bighorn sheep fecal piles were collected by field staff during 1992-94 in the ^Nnorth and ^Ssouth ^Uunits of Badlands National Park. Samples were kept in frozen storage until analyzed. A sample representing a population's diet on a specific area during a certain time period can be obtained by sub-sampling (Anthony and Smith 1974). Based on collection date, fifty-two samples were selected as representative sub-sample. These samples were microhistologically analyzed to estimate bighorn sheep dietary selection. A detailed park vegetation map was not available that would have allowed estimates of actual forage preference. The analysis included all plant genus found at a relative frequency 10% or more in the sampling. A multi-response permutation procedure (Biondini 1988 and Mielke 1991) was used to test for differences in dietary composition between the north and south units.

Effect of Fire on Forage Quality

Four elevated sod buttes and four groups (three tables per group) of lower sod tables were chosen as sites for burning treatments. Each site was divided into three treatment areas. One-third of each site was burned during the fall of 1992, one-third was burned during the spring of 1993, and one-third was left as a control. A pretreatment sampling was performed in August of 1992 on the four major buttes. Biomass and species composition were taken on the various treatment areas prior to the experiments through a sample of 8-10 randomly-located m² plots per treatment.

Post-burn plots were located on each treatment for biomass sampling. There were 18 plots on each of the four major buttes (6 plots per treatment) and 12 plots on each of the low sod table sites (4 plots per treatment). Using a clipping frame, a .25 square meter area was clipped both inside and outside the exclosure. Clipped plants were separated by species, dried and weighed. For 5 selected forage plant species (*Agropyron smithii*, *Bouteloua gracilis*, *Carex eleocharis*, *Carex filifolia*, and *Stipa comata*), 4 variables were measured: dry weight, percent nitrogen, percent protein, and dry matter digestibility. Multivariate analysis of variance (MANOVA) tests was used to determine, for each species and each measured variable, whether the difference between the two years was constant across all the treatments. ANOVA tests were used to determine for each species whether the measured variables showed a significant treatment effect within a year. Biomass samples were taken twice during both the 1993 and 1994 growing season, as well as once at the end of the winter of 1993-94. The first clipping was done during the peak of cool season (C-3) plants, the second for warm season (C-4) plants, and the third was a winter-offtake clipping.

Habitat Selection

This analysis presents data collected from bighorn ewes in the ^North ^Unit of Badlands National Park. Six bighorn ewes were captured and collared in March 1992. Ground crews gathered data on bighorn sheep from June 1992 to November 1994 (n=554). Habitat data was recorded on collared and randomly encountered ewe

groups. The following data was recorded: location, group size, group composition, behavior, topographic position, cover type, forage type, slope (in degrees from horizontal), and distance to escape terrain. Seasonal selection was determined using ANOVA and chi-square analysis for 4 habitat characteristics: topographic position, cover type, distance to escape terrain, and slope. Five seasonal divisions were chosen to correspond with observed seasonal differences in behavior: spring (March-April), lambing (May-June), summer (July-September), rut (October-November) and winter (December-February).

ANOVA was used to determine if there were significant differences between the seasonal means of slope and distance from escape terrain. Chi-square tests were used to determine whether bighorn sheep locations in cover type and topographic positions differed seasonally. Chi-square tests were then used to test for differences between habitat characteristics of adjoining seasons: spring-lambing, lambing-summer, summer-rut, rut-winter, and winter-spring.

RESULTS

Lungworm Larvae Incidence

Lungworm larvae levels were higher in the ^N north ^U unit than ^S south ^U unit (Figure 1, $P < 0.05$, north unit mean = 12.1 LPG, south unit mean = 3.9 LPG). Lungworm larvae were detected in the ^N north ^U unit samples more often (94% $n=34$) than the ^S south ^U unit samples (60% $n=15$). The yearly rainfall total for 1992 was more than 50% greater

than the yearly rainfall for 1993 (65 cm. and 42 cm. respectively), but seasonal levels of lungworm in the ^N north ^U unit did not vary ($P=0.94$).

Diet Selection

Relative density of plant fragments in the fecal samples differed significantly between the ^N north and ^S south units of the park (Figure 2, $P<0.01$). *Agropyron* was identified at higher densities in the ^N north unit than the ^S south unit ($P<0.01$, 30.2% and 10.3% respectively). Conversely, *Stipa* was found to be much less prevalent in the ^N north unit than the ^S south unit ($P<0.01$, 14.4% and 34.2% respectively). The ^{five} other genus that occurred in different relative frequencies in the ^N north and ^S south units are: *Carex* ($P<0.05$, 17.9% and 7.7%), *Artemisia* ($P<0.01$, 3.2% and 8.3%), *Astragalus* ($P<0.01$, 2.5% and 6.0%), *Symphoricarpos* ($P<0.01$, 2.9% and 5.5%), and *Yucca* ($P<0.01$, 1.5% and 4.7%).

Effects of Fire on Forage Quality

Few significant differences were found in the measured variables for two years after the burns. The mean dry matter digestibility values for *Stipa comata* varied between years by treatment (Figure 3, $P<0.05$). During the first year after the burns, the mean dry matter digestibility values for *Stipa comata* were higher in the fall treatment, followed by the control treatment, and then the spring treatment ($P<0.05$; Fall=46.8%, Control=44.1%, Spring=42.0%). Also in the first year following the burns,

mean values for percent nitrogen of *Agropyron smithii* were higher in the spring treatment, followed by the fall treatment, and then the control treatment ($P < 0.05$; Spring=0.82%, Fall=0.72%, Control=0.66%). Planned future work includes the analysis of forage biomass data taken during pretreatment sampling and winter offtake sampling.

Habitat Selection

During lambing, ewe groups were most often found in rugged topographic locations (midslope, 38.8%; peak/ridge, 24.6%). While during spring, ewe groups utilized the elevated sod buttes most often (48.8%) and were rarely found on peak/ridge sites (7.0%)(Table 1). The topographic positions at which ewe groups were observed during the winter differed from both rut ($P < 0.001$) and spring ($P < 0.001$) locations. In winter, ewe groups were often seen on elevated sod buttes (42.4%) and badland slumps (26.5%). Whereas during spring, ewe groups were spotted infrequently on badland slumps (11.6%). Observations of ewe group topographic position during the rut indicated the most balanced use of topography by the ewes with only one position above 20% (midslope, 20.7%).

Bighorn ewe groups were located in four major cover types that differed by season (Table 2). There was a difference ($P < 0.05$) in cover type locations between spring and lambing. In spring, ewe groups were found less often on areas without vegetation (39.5%) and more often on grass cover (53.5%) than during lambing

season (no vegetation = 39.5%, grass = 37.3%). Percentages of summer cover types were significantly different ($P < 0.001$) than during the rut. Cover type locations with no vegetation constituted a higher amount in summer (51%) than during rut (24.4%). During rut, groups were found more often in juniper (17.1%) and grass (54.9%) cover types than those for summer (2.9 and 37.5%, respectively). Winter locations were different than spring ($P < 0.01$). Winter cover type locations in juniper were higher (18.4% compared to 5.8%) than spring or any other season. Spring locations in no-vegetation were higher (39.5% compared to 22.4%) than winter.

Distance to escape terrain of ewe groups varied by season (Table 3, $P < 0.001$). The average distance that bighorns were observed from escape terrain was shortest during the lambing period (5.1 m $SD \pm 2.7$) and longest during the rut period (29.6 m $SD \pm 3.5$). The slope of the terrain at which bighorns were observed varied seasonally ($P < 0.001$). Ewe groups were observed on the steepest slopes during lambing season (37.7° $SD \pm 1.9$), and on the mildest slopes during winter (14.5° $SD \pm 1.9$).

DISCUSSION

Lungworm Larvae Incidence

Historically, bighorns in Badlands National Park probably migrated longer distances and dispersed more, thus reducing disease and parasite loads resulting from sedentariness (Bailey 1980, Risenhoover et al. 1988). We found a higher

relative infestation of lungworm in the North Unit ~~herd~~ which may be explained by the higher bighorn density in the ^N ^U ~~north~~ ~~unit~~. Variation in annual precipitation rates did not produce a significant seasonal variation in lungworm infestation

Diet Selection

The diets of bighorn sheep in the ^N ^U ~~north~~ and ^S ^U ~~south~~ ~~units~~ of Badlands National Park were similar in their plant diversity, but were dominated by different genus. It is reasonable to assume that plant availabilities are going to be different in the two units due to natural variations in soils, topography, and hydrology. Different plant availabilities would alter diet selection. Also, the population density of the ^S ^U ~~south~~ ~~unit~~ is much lower than the ^N ^U ~~north~~ ~~unit~~, which may allow the bighorns in the ^S ^U ~~south~~ ~~unit~~ to seek out more highly preferred forage species. Only after completion of a vegetation map and sampling of plant availabilities can the dietary preferences of the north and south unit be determined.

Effects of Fire on Forage Quality

We documented few positive effects due to the burning treatments. These results were unexpected. Other authors have noted that protein concentrations and digestibility of grasses are quantitatively more enhanced by burning. Fibrous

constituents, which reduce digestibility, are often decreased (Allen et al. 1976). In our study, the only advantages accrued from burning were short-term increased nitrogen concentrations in the single most common bighorn forage species (*A. smithii*) and increased digestibility from the fall burn only in the second-most utilized forage genus (*Stipa* spp.)

Habitat Selection

Bighorn sheep typically select open grassland habitat near steep, rocky escape terrain (Geist 1971; Wakelyn 1987; Risenhoover and Bailey 1985; Fairbanks et al. 1987). Ewe groups selected for different topographic positions, cover types, distance to escape terrain, and slope according to the season. In spring, ewes were most often found on elevated sod buttes. Spring green-up would likely entice ewes onto these grassy buttes to forage on nutritious early plant growth. Goodson (1991) found that ewes selected areas of high green-up concentration which became visible after snow-melt. In a study of bighorns at Trout Peak, Hurley (1985) noted that sheep preferred grassland type vegetation during the spring. Foraging efficiency of sheep was positively associated with proximity escape terrain and positively associated with visibility (Risenhoover and Bailey 1985). Predictably, foraging efficiency should be high on these treeless sod covered buttes. Ewes have been observed to select rugged steep terrain for their lambing areas (Geist 1971) which offer ample protection from predators. Ewes travel to these areas prior to parturition (Festa-Bianchet 1988). Ewe-juvenile groups are often found on rugged precipitous terrain (Gionfriddo and

Krausman 1986). During lambing season in the Badlands, ewe groups were located in extremely remote areas. Ewe groups displayed an affinity for midslopes and peak/ridge areas during the summer. Perhaps some of the locations in these steep, bare areas were a consequence of seeking out shade. The steep slopes offer shade and were devoid of vegetation. Temperatures in the Badlands during the summer can exceed 38°C and sheep have been observed bedded in shaded areas. In Arizona, Gionfriddo and Krausman (1986) reported that bighorns sought out shade possibly as a means of moderating the effects of high temperatures. Summer topographic positions and cover types were quite similar (Tables 1 and 2) to lambing season and the average slope was still quite steep. This effect was probably due to ewes with lambs maintaining maternal ranges while ewes without lambs moved into summer habitats (Geist 1971).

The period of rut in Badlands included the months of October and November. During this period, ewe groups exhibited the greatest average distance from escape terrain. By moving farther away from escape terrain, ~~E~~^ewe groups were able to spend more time in grass cover types (Table 2). Group locations during rut were the most evenly distributed across the topography positions. This may have been in part due to a behavioral response of being chased by rams. During winter, ewe groups were most often observed foraging on elevated sod buttes. The sod buttes were exposed to wind, minimizing snow accumulation. Tilton and Willard (1982) found that, in winter, bighorn sheep prefer open areas in which forage is most available. Locations of groups on elevated sod tables may have also been influenced by their behavioral adaptation of feeding during daylight (generally midday during the winter) (Geist

1971). This behavior helped in reducing energy costs. Also, ewe groups were frequently seen on badland slumps in winter. Juniper growths were often found on slumps on southern exposures of elevated sod buttes. Arnett (1990) reported that sheep tended to avoid north aspects in winter. The badland slumps and juniper cover may have provided some protection from the strong, cold winds during the winter. Additionally, the slumps likely provided adequate forage because the juniper patches were usually interspersed with grassy areas.

MANAGEMENT IMPLICATIONS

The bighorn sheep of Badlands National Park occupy a prairie-grassland environment, much different than the montane environment inhabited by most well-studied bighorn herds. Analysis of lungworm infection was problematic. There is no clearcut evidence that fecal larvae counts correlate with infection intensity in bighorns (Festa-Bianchet 1991). No evidence suggests that lungworm infection is associated with pneumonia (Festa-Bianchet 1991). Also, larvae counts are an inaccurate indicator of herd health because counts may be influenced by numerous factors including pellet weight, daily fecal production, reproductive effort, nutritional stress, immune system status, and body condition (Festa-Bianchet 1991). The lungworm larvae counts contained in this report may imply a higher infection rate in the ^N north unit, but should be interpreted with discretion.

Differences in bighorn sheep dietary content between the ^N north and ^S south units indicate a critical need for a complete community vegetation map for Badlands

National Park, so that the influence of forage availability can be properly evaluated. Fire effects were minimal for our burn study in a mixed-grass prairie. The only detected benefits were associated with the green up immediately following the burn. These results are in disagreement with other work that examined the effects of fire on bighorn sheep habitat in Rocky Mountain habitats. In our study of habitat use, bighorn ewe groups exhibited selectivity in their habitat requirements on a seasonal basis. Our results emphasize the varying seasonal requirements of bighorn ewes and the need to manage for year-round habitat requirements.

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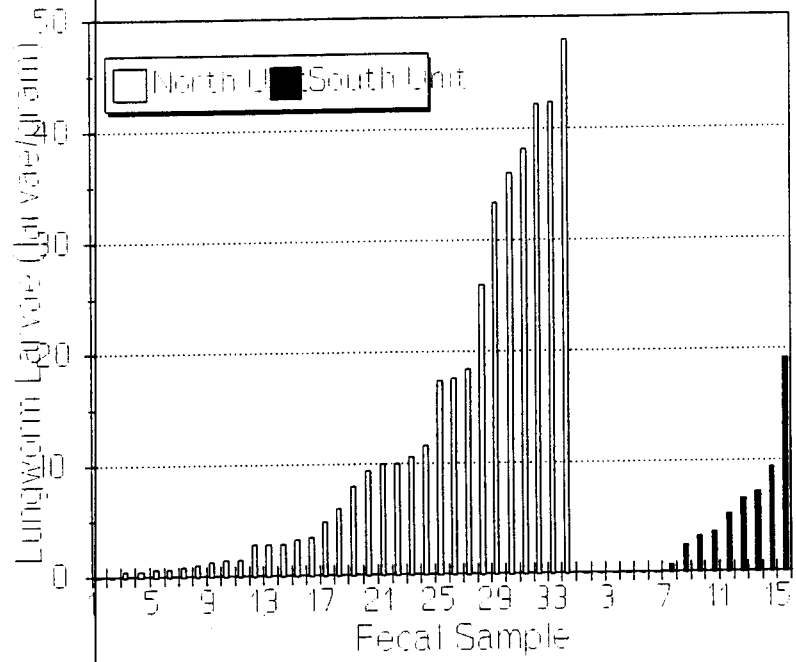


Figure 1. Incidence of lungworm larvae in fecal samples collected in the north and south units of Badlands National Park, SD.

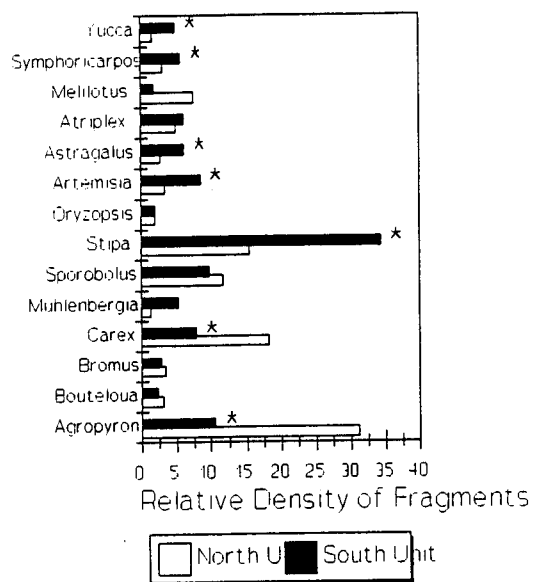


Figure 2. Relative density of plant fragments from microhistological analysis of bighorn sheep fecal samples collected in Badlands National Park, SD. Asteriks (*) denote genus with significantly different relative densities in the north and south units.

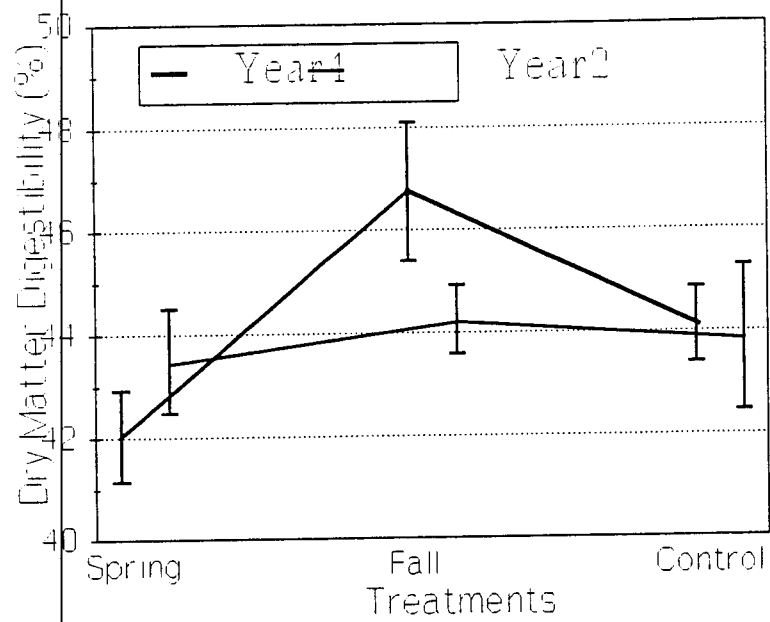


Figure 3. Percent dry matter digestibility of *Stipa comata* biomass samples collected during the two years following burn treatments in the north unit of Badlands National Park, SD.

Table 1. Percent of ewe group locations in topographic positions by season in the North Unit of Badlands National Park, SD.

Topographic Position	Spring ^{a,c}	Lambing ^a	Summer	Rut ^b	Winter ^{b,c}
Peak/ridge	7.0	24.6	18.3	13.4	7.5
Midslope	22.1	38.8	27.9	20.7	10.9
Badlands Base	4.7	3.0	2.9	6.8	1.0
Badlands slump	11.6	9.7	13.5	17.1	26.5
Elevated Sod Butte	48.8	17.2	21.2	17.1	42.4
Lowland Sod Table	4.7	1.0	4.8	3.7	2.0
Vegetated Lowlands	0.0	2.2	3.8	13.4	8.8

^a Spring versus lambing season $P < 0.0001$.

^b Rut versus winter $P < 0.0001$.

^c Winter versus spring $P < 0.001$.

Table 2. Percent of ewe group locations in cover type per season in the north unit of Badlands National Park, SD.

Cover Type	Spring ^{a,c}	Lambing ^a	Summer ^b	Rut ^b	Winter ^c
No Vegetation	39.5	56.0	51.0	24.4	22.4
Juniper	5.8	2.2	2.9	17.1	18.4
Rubber Rabbitbrush	1.0	2.2	6.7	2.7	1.4
Grass	53.5	37.3	37.5	54.9	55.8

^a Spring versus lambing season $P < 0.05$.

^b Summer versus rut $P < 0.0001$.

^c Winter versus spring $P < 0.01$.

Table 3. Average percent distance (m) to escape terrain and average slope (degrees from horizontal) in the ^North ^Unity of Badlands National Park, SD.

Season	Spring	Lambing	Summer	Rut	Winter
Distance to Escape Terrain ^a	9.0 ± 3.4	5.1 ± 2.7	14.0 ± 3.1	29.6 ± 3.5	19.6 ± 2.6
Slope ^a	23.1 ± 2.4	37.7 ± 1.9	29.3 ± 2.2	19.8 ± 2.5	14.5 ± 1.9

^a Both variables varied significantly between seasons ($P < 0.001$).