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Habitat Selection and Sexual Suggestion of Rocky Mountain Bighorn Sheep in Custer State Park, South Dakota

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HABITAT SELECTION AND SEXUAL SEGREGATION OF ROCKY MOUNTAIN BIGHORN SHEEP IN CUSTER STATE PARK, SOUTH DAKOTA

BY

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This thesis is approved as a creditable and independent investigation by the candidate for the degree Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT: One hypothesis which explains segregation between Rocky Mountain bighorn ram and ewe herds was examined using the Custer State Park bighorn sheep population. Three predictions of this hypothesis, similarity of habitat types, similarity of habitat utilization, and high home range fidelity, were assessed using physical habitat measurements and locations of radio-tagged individuals of both sexes. Habitat types were similar, as classified with discriminant analysis, with respect to each type, across all of the sheep ranges. Members of each sheep herd maintained high fidelity to their respective home range. Habitat utilization differences were inconsistent among the herds, regardless of sex, except for selection against doghair ponderosa pine habitat type by all herds. Utilization of feeding and resting areas were also selected or avoided inconsistently, except for avoidance of doghair ponderosa pine for both resting and feeding, and also ponderosa pine/no understory for feeding. Mixed grass/forb, ponderosa pine/grass forb, and riparian habitat types were used most frequently for feeding, and steep rocky/ponderoasa pine most frequently for resting. Rams foraged at significantly greater distances ($F = 4.99$, $p = 0.0009$) from escape terrain than ewes although group size of rams was always small (1-5 individuals) and ewe group sizes ranged from small to large (up to 29 members). These results supported 2 of the 3 hypothesis predictions; similarity of habitat types and fidelity of home range. However, the most important prediction, similarity of habitat utilization between the sexes, was not supported and consequently the hypothesis of minimizing habitat competition between the sexes was rejected as not providing a complete explanation for sexual segregation. An alternative hypothesis, where rams and ewes segregate in order to reduce agonistic interactions between them, is presented. Future directions to more completely test the competing hypotheses which explain sexual segregation in bighorn sheep are suggested.

INTRODUCTION

Spatial segregation between Rocky Mountain bighorn sheep (Ovis canadensis canadensis) ram and ewe herds has been documented by Geist (1971), Geist and Petocz (1977), Shank (1979), Morgantini and Hudson (1981), and Hogg (1983), where ram herds consist of mature males approximately 4 years old and older and ewe herds are comprised of all other individuals. Geist (1971), Shank (1979), and Hogg (1983) have shown that segregation occurs year-round except during the breeding season (November and December) when the sexes congregate on a traditional breeding range (cf. Geist 1971, p 209). These studies also have shown that the sexes remain separated during the winter, when segregation should be least likely. During winter, resources, particularly forage, are most limiting and when the sexes would be expected to remain congregated after the breeding season, such as at available foraging sites. However, both Geist and Petocz (1977) and Morgantini and Hudson (1981) reported that the sexes remained segregated on a continuous winter range, even during severe winters.

Four hypotheses have been developed to explain sexual segregation of bighorn sheep. Shank (1979)

believed sexual segregation was a result of differential habitat requirements due to sexual dimorphism. Segregation has been suggested as an anti-predator strategy for males which are physically weakened after the breeding season (Geist and Bromely 1978). Morgantini and Hudson (1981) suggested that sexual segregation reduces frequency of agonistic interactions among rams during the post-breeding season and maximizes fitness of rams by conserving energy when reproduction is not possible. Geist and Petocz (1977) explained segregation as a mechanism for rams to minimize habitat competition with pregnant ewes and their prospective lambs, thus increasing survival of lambs, and thereby maximizing reproductive fitness of rams.

Morgantini and Hudson (1981) concluded that reduction of agonistic behavior among rams after the breeding season provided the best explanation for sexual segregation during winter, and each of the other hypotheses could be considered additional benefits accrued as a result of this behavior. However, this hypothesis is inadequate to explain why segregation is maintained during the rest of the year when energy intake is maximum and behaviors among rams would be least detrimental. The hypothesis of increased predation risk proposed by Geist and Bromely (1978) is also inadequate

to explain maintenance of segregation between the sexes during the summer and fall when body condition of the sexes should be in best condition. The hypothesis by Shank (1979) adequately explained why segregation may be maintained throughout the year, but because differential habitat requirements were not demonstrated, he concluded that the sexes did not partition their range in a manner that best satisfied sex-specific requirements. Only the hypothesis of Geist and Petocz (1977) of minimizing habitat competition between the rams and ewes best explains why segregation should be maintained throughout the year, except during the breeding season.

Geist and Petocz (1977) emphasized reduced competition for forage resources, however habitat provides other resources, some of which may be competed for (Anderson and Shugart 1974). Habitat is defined primarily as a place where an organism lives and secondarily as how that place is characterized (Wittenberg 1981, Ricklefs 1973, Brown and Gipson 1983). Bighorn sheep habitat may be divided into a physical component and a forage component, with the forage component described by the composition of forage species (eg. grasses and forbs), and the relative importance each contributes to the diet, and the physical component, which consists of both biotic and abiotic descriptors and

their spatial distributions; in essence, the visual appearance of the habitat. It is unknown whether intersexual competition for the structual component or the forage component is more important in bighorn sheep. However, Shannon et al. (1975), Morgantini and Hudson (1981), Geist (1971), and Geist and Petocz (1977) showed that habitat structure was important in explaining the distribution of ram and ewe herds, and Geist (1974) considered the 3-dimensional structure of habitat to be an important factor in ungulate social evolution.

The objective of this study was to examine the predictions of the hypothesis that segregation reduces habitat competition between ram and ewe herds in bighorn sheep during the summer and fall. The predictions were, if rams and ewes segregate in order to reduce habitat competition between them, then they should: 1) occupy home ranges which share similar physical characteristics for each habitat type, 2) utilize those types with similar frequencies, and 3) maintain fidelity of home range occupation both spatially and temporally. In this study, habitat characterization focused on the physical component.

The bighorn sheep population found in Custer State Park (CSP) is particularly well suited to examining this hypothesis. The present population is derived from 22

individuals (15 ewes, 7 rams) transplanted from Wyoming in 1964 (W. Jackson unpubl. rep. 1981). Between 1964 and 1985, the herd increased to a level of at least 90 animals and separated into 6 distinct herds. Because the currently occupied areas were vacant of bighorn sheep at the time of the transplant, an assumption was made that these separate herds have established their home ranges to best satisfy each herd's habitat choice. Given that the sheep had free choice to establish a home range anywhere within the park boundaries, their observed home ranges should reflect what they considered as the optimal areas to define a home range. Additionally, the ranges of all herds are assumed to be qualitatively equivalent, where at least the minimum amount of nutrition is available to all members of this bighorn sheep population.

STUDY AREA

Research was conducted in CSP, which is located in the southeast portion of the Black Hills, South Dakota. Bighorn sheep ewes primarily inhabit French Creek Canyon, located in the central portion of the Park, and rams occupy ranges peripheral to those of the ewes (Fig. 1). French Creek Canyon is approximately 19 km long and ranges from 70 to 140 m in depth. It is characterized by steep, rugged walls with adjacent rolling meadows and ponderosa pine (Pinus ponderosa) forests. The Park headquarters region, located in the center of the Park, contains a few meadows and steep, forested hills with rock outcrops. The southwestern portion of the Park is characterized by hilly, forested terrain with some extensive rock outcrops adjacent to a few relatively large meadows. The southeastern portion of the Park south of and adjacent to French Creek Canyon is characterized by less steeply rolling, but forested, terrain with few rock outcrops and few meadow areas. Physiographically, the headquarters region and southwest area appear similar, while the southeast area is the least rugged of any of the areas used by CSP bighorn sheep. Elevations within CSP bighorn sheep ranges vary from 1160 to 1707 m, rising steadily from the southeast to the north and west.

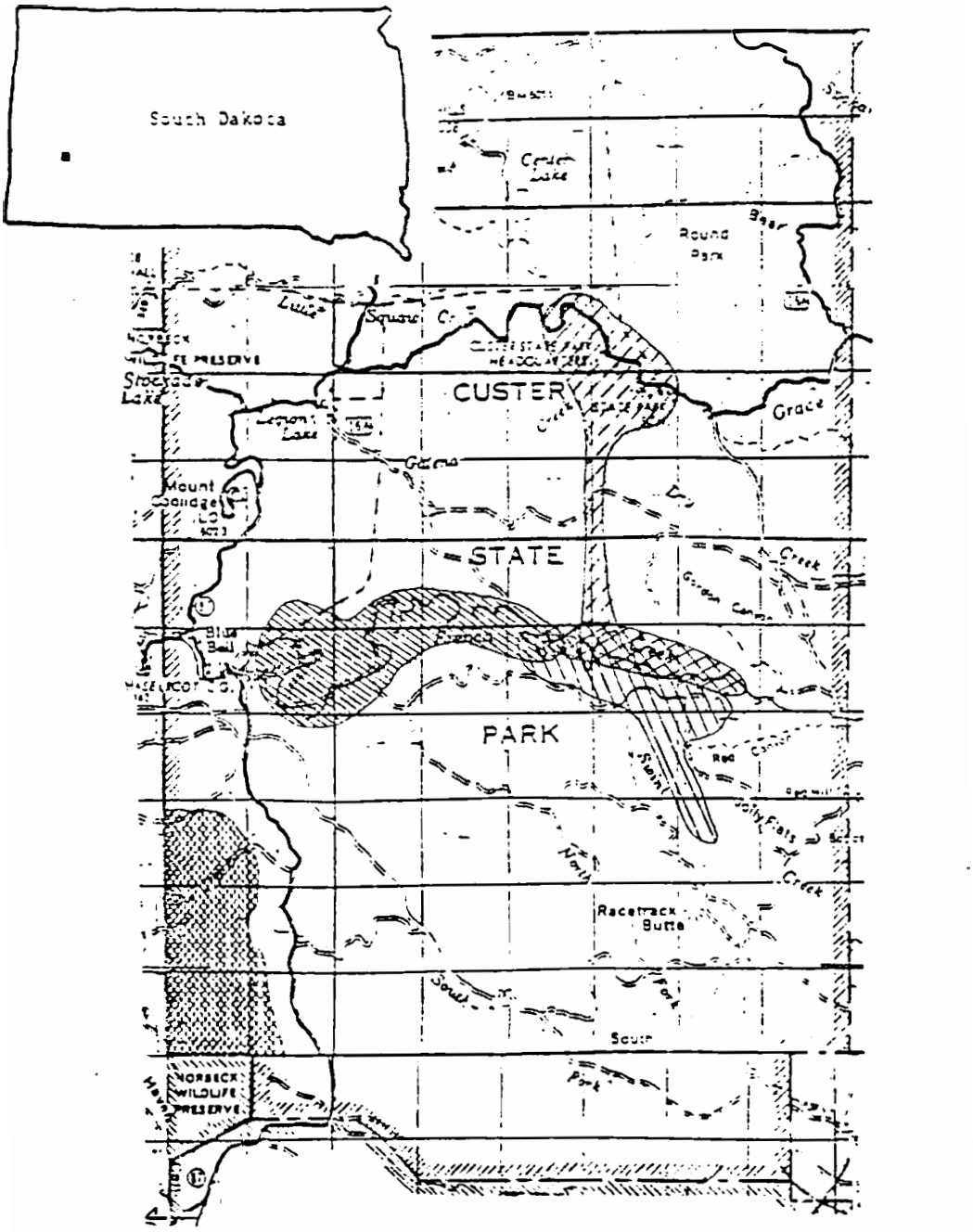

Figure 1. Location of French Creek Canyon and ram and ewe group home ranges in Custer State Park, South Dakota, 1985. Ewe groups: Grace Coolidge, East End and Grace Coolidge, West End. Ram groups: Southeast, Southwest. Scale: 0—— 1 miles.

METHODS AND MATERIALS

The 3 ewe herds were designated east end (EE), west end (WE), and Grace Coolidge (GC) herds (Brundige 1985). Divisions for the 3 ram herds were northeast (NE), southeast (SE), and southwest (SW). The summer/fall ranges of each herd are indicated in Figure 1. Only the GC range extensively overlapped that of the EE herd on French Creek Canyon and members of both ewe herds intermingled in this overlap area (Brundige 1985). Otherwise, there was almost no range overlap among the herds and individuals remained associated with their respective herd and range. Accordingly, sampling schemes for vegetation and movements were divided with respect to each sheep herd.

Division of Habitats

Habitats for the sheep herds had previously been divided into 7 types based on visual appearance (Brundige 1985). These divisions were based on presence or absence of trees, presence or absence of understory, degree of slope, and degree of rockiness. Mixed grass/forb habitat type was designated for meadows and consisted of mostly grasses with some forbs, usually no rocks present, and no trees present. Riparian habitats were those characterized by vegetation found near streams and could include grasses, forbs, rocks, and a mixture of several

deciduous tree species and/or ponderosa pine. A permanent water source was necessary to maintain riparian areas. Ponderosa pine/grass forb was similar to mixed grass/forb except that ponderosa pine, or, rarely, bur oak (Quercus macrocarpa), was present. This habitat was typical of a coniferous parkland. The ponderosa pine/no understory category consisted of a ponderosa pine forest with only an occasional forb or grass present, few rocks, and was usually located on slopes of less than 40%. Doghair/ponderosa pine habitats were similar to ponderosa pine/no understory, except they were much more dense and where found contained trees of a uniform height. The characteristics of this habitat could best be described as a stand of ponderosa pine whose stems average less than 15 cm in diameter at breast height (DBH), grow 1.5 m or less apart, and average approximately 6 m in height. Rocks could be present but no understory was present. Steep rocky/grass forb areas were typical of open slopes usually steeper than 35%, with rocks, but no trees present. Steep rocky/ponderosa pine was similar to steep rocky/grass forb except ponderosa pine was present. A description of plant species composition for each habitat type is given by Brundige (1985) for the EE and GC ranges for 1984.

Characterization of Habitat Types

Physical characteristics for each of the above habitat types were sampled in all of the sheep ranges. For each range, 3 or 5 sampling plot centerpoints were chosen randomly for each habitat type. Within each sheep range, centerpoints were chosen by assigning a number to every sheep location in each type obtained during July, 1985. Numbered locations were randomly chosen to determine to define a sampling plot centerpoint. In cases where fewer than 3 sheep locations were available for a particular habitat type at time of sampling, centerpoints were chosen within types without locations near types which had sheep locations. The number of centerpoints (3 or 5) per habitat was subjectively determined by the relative abundance of that habitat for a given range. For types which had relatively small total areas, 3 points were selected; otherwise 5 were used. Three sampling plot centerpoints were used for all of the habitat types in the northern portion of the GC range located in the Park Headquarters region of CSP (Fig. 1). Plot centerpoints were positioned within the respective habitat type to avoid the inclusion of areas that appeared to be transition zones. Thus, each centerpoint was assumed to be located in a homogeneous sample of the habitat type selected.

At each sampling centerpoint, a 10 x 10 m plot was delineated with the edges lying in the 4 cardinal compass directions. Within this plot, tree density and basal area, ground cover, overhead canopy, horizontal obstruction, slope and aspect were measured. Elevations were estimated to the nearest 10 m from U. S. Geological Survey (USGS) 7.5 min. quadrat maps.

Mean tree density was estimated by counting the number of stems for each species in each habitat type and converting this number to stems/ha. Similarly, mean tree basal area was estimated by measuring DBH to the nearest 0.5 cm, converting DBH to basal area, and expressing as cm^2/ha.

Overhead canopy was estimated using a convex spherical densiometer (Forestry Suppliers, Inc. Jackson, MS) placed in the center of the plot and using 4 readings. The densiometer was kept level by attaching it to a camera tripod.

Mean horizontal obstruction of vision was estimated by using a density checkerboard, 1.5 x 1.5 m and marked in alternating black-and-white, 15 cm squares giving a total of 100 squares. The number of squares covered were counted and the 4 readings were averaged to give an estimate of horizontal obstruction for the plot. A square was considered covered if at least 1/2 of it was

obstructed from vision. The board was read from a kneeling position to approximate the height of eyesight for an average bighorn sheep (Risenhoover and Bailey 1985). The board was placed at a distance of 15 m and read from the center of the plot in each of the 4 cardinal directions.

Ground cover was estimated using line transects and a 20 x 50 cm quadrat (Daubenmire 1959). Within each sampling plot, 4 - 5 m transects were randomly placed in one of 8 compass directions (N, NE, E, SE, S, SW, W, NW). No transect was allowed to overlap any other transect. Five quadrats were placed parallel and next to each transect line at 1 m intervals. Placement of the quadrat with respect to the side of the transect line was determined by a coin toss. A total of 20 quadrats for each sampling plot was used.

Ground cover was divided into 7 categories: grass, forb, shrub, log, duff, rock, and bare ground. The grass category was comprised of grasses and grass-like forms including Carex spp. Forbs were defined as herbaceous broadleaved species. Shrubs included plants with more than 1 woody stem and ponderosa pine seedlings less than 20 cm tall. Dead and downed trees or branches greater than 3 cm in diameter were classified as logs. Duff included dead plant parts and any dead woody

material less than 3 cm in diameter. This category consisted mostly of shed ponderosa pine leaves. Rocks were considered as such if they were 3 cm or greater in their longest axis. The bare ground category included mostly bare soil and rocks less than 3 cm. Each of these categories were measured by percent cover within the quadrat.

Location Sampling

Individually radio-marked sheep were located from July through October 1985. Five ewes from the GC herd, 4 from the EE herd, and 8 from the WE herd were radio-collared. One ram each from the SE, SW, and NE ram herds had a solar transmitter attached to its ear. Daylength was divided into 2 periods: early (0500 hrs to 1300 hrs), and late (1300 to 2100 hrs). For ewes, 4 locations per daylength period per herd were determined using randomly selected, radio-marked sheep. A radio-tagged ram was located up to 4 times in each daylength period that it was sampled. The interval between successive locations for all herds was a minimum of 1 hour.

Habitat type and map location, as designated by Universal Transverse Mercator (UTM) longitude and latitude on USGS 7.5 min. quadrat maps, were recorded for each location of a radio-marked sheep. Also recorded were percent slope, aspect, elevation, group size, and

age and sex composition of any associated sheep. Activity categories, including resting, feeding, moving, nursing, and standing, were observed in order to calculate activity budgets and determine whether there was any differential habitat use among the sheep herds for each activity considered.

Seasonal Home Range Estimation

Seasonal home ranges for each herd were estimated from locations of radio-marked sheep in each herd. The minimum polygon method was used to statistically estimate a home range area and boundaries. Locations that caused the estimated area to include portions of land where sheep were never seen, or which lacked any evidence of their presence, were not used. Such locations were assumed to be excursions of individuals from the respective sheep herd (Geist 1971) and therefore they were not included. After home range boundaries were delineated onto USGS 7.5 min. quadrat maps using the minimum polygon method, topographic features were subjectively included to define the home range boundaries and inclusive habitat types used in utilization estimation. Using this method, the home range usually included an entire hillslope to the top of a ridge rather than only partial hillslopes or valleys. The subjectively delineated home range encompassed the entire

area estimated by the minimum polygon method and is probably a more realistic representation than the minimum polygon method itself (MacDonald et al. 1979).

Estimating Proportion of Use

The proportion of each habitat type found in each sheep herd home range was measured from USGS 7.5 min. quadrat maps. Habitat types were outlined from aerial photographs onto clear acetate sheets, and then traced onto the quadrat maps using a Map-O-Graph (Art-O-Graph, Minneapolis, MN) to correct for scale and photograph distortion. These areas were measured in cm^2 using an area meter (Model LI-3000 Area Meter, Lambda Instruments Corporation) and converted to hectares. Precision of the meter was ± 0.02 cm^2. Proportion of each habitat area was calculated by dividing the total area of the home range into the area covered by a habitat type. The mean of the slopes for each type was used as a correction factor for proportion of actual area covered by each habitat, since slope means for each type across all ranges were found to be not statistically different ($F = 1.54$, $p = 0.0756$, $df = 22$).

Selection or avoidance was estimated using the proportion of area for each habitat type within the home range, and the proportion of locations, according to the methods of Neu et al. (1974) and Byers et al. (1984).

Only those locations used to estimate the home range area were used in estimating proportion of use.

Geist (1971) noted that resting and feeding areas may be particularly important in determining suitability of ranges for sheep. Thus, frequencies for each of these activities were compared among the 7 different habitats of each sheep herd to determine any differences in utilization of these habitats. Risenhoover and Bailey (1985) have also discussed the importance of feeding areas with respect to group size and distance from escape cover, where escape cover is defined as precipitous, rocky terrain (Geist 1971). Accordingly, distance from escape cover at first sighting for a location were visually estimated and compared among sheep herds for each type used for feeding or resting.

Statistical Analyses

Habitat types were analyzed using ground cover and tree plot measurements and compared using discriminant analysis. Means for each variable from each sampling plot were used as observations for this analysis. The only variable excluded from these analyses was shrub cover, since coverage was less than 5% in all habitats sampled. Mean area of each habitat type and mean distances to escape cover were compared using analysis of variance (ANOVA, Sokal and Rohlf 1981). Frequency

comparisons of numbers of sheep groups observed among habitat types were made using chi-squared test of independence (Sokal and Rohlf 1981). Discriminant analysis and ANOVA were performed using appropriate programs contained in Statistical Analysis Systems (Goodnight 1986) software. Significance levels for ANOVA and chi-squared tests were 0.05, and 0.10 for discriminant analysis.

For the methods of Neu et al. (1974) and Byers et al. (1984) for estimating habitat utilization, expected proportion of usage (p_{io}) was calculated by dividing total range size into each respective habitat area. Expected frequencies of utilization were then found by multiplying p_{io} times the sum of the number of observations. Significance level to determine utilization greater than, less than, or in proportion to habitat type availability was 0.05.

RESULTS

Only 5 locations were obtained for the NE ram herd during the study period. Therefore, data for this herd were excluded from habitat and utilization analyses.

Division of Habitat Types

A total of 120 vegetation plots were measured, which included all habitat types found in each sheep range (Table 1). Each type was classified as distinct from any other type within each sheep herd range (Table 2). Also, a type found in one range was not classified differently from that same type which occurred in any of the other ranges. These results indicated that observed differences among the habitat types both between and within the sheep ranges were also differentiated quantitatively, according to the variables measured, for not less than 93% of the observations for each type. Amount of overlap and relative degree of heterogeneity for each habitat type using canonical representations of the first and second discriminant functions are shown in Figure 2. Habitat types for all ranges combined are characterized in Figures 3 through 5. Habitat type descriptions for each sheep herd range are shown in Appendix I.

Table 1. Number of vegetation sampling plots for each habitat type located within each sheep herd range in Custer State Park, SD, from August through September, 1985.

	Sheep Herd					
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd	Total
mixed grass/ forb	5	5	3	5	5	23
ponderosa pine/ no understory	5	5	3	5	5	23
ponderosa pine/ grass forb	5	5	3	5	5	23
riparian	5	5	3	0	3	16
steep rocky/ grass forb	6	2	0	3	3	14
steep rocky/ ponderosa pine	5	5	3	3	5	21
Total	31	27	15	21	26	120

Table 2. Discriminant analysis classification summary for each habitat type for all sheep ranges included in Custer State Park, SD, from August through September, 1985. Habitat types are: MF - mixed grass/forb, PB - ponderosa pine/no understory, PG - ponderosa pine/grass forb, RI - riparian, SG - steep rocky/grass forb, and SP - steep rocky/ponderosa pine.

	Number of observations and (percents) classified into types						
From Type	MF	PB	PG	RI	SG	SP	Total
MF	22 (95.65)	0 0	0 0	0 0	1 (4.35)	0 0	23
PB	0 0	22 (95.65)	1 (4.35)	0 0	0 0	0 0	23
PG	0 0	1 (4.35)	22 (95.65)	0 0	0 0	0 0	23
RI	1 (6.25)	0 0	0 0	15 (93.75)	0 0	0 0	16
SG	0 0	0 0	0 0	0 0	14 (100.00)	0 0	14
SP	0 0	1 (4.76)	0 0	0 0	0 0	20 (95.24)	21

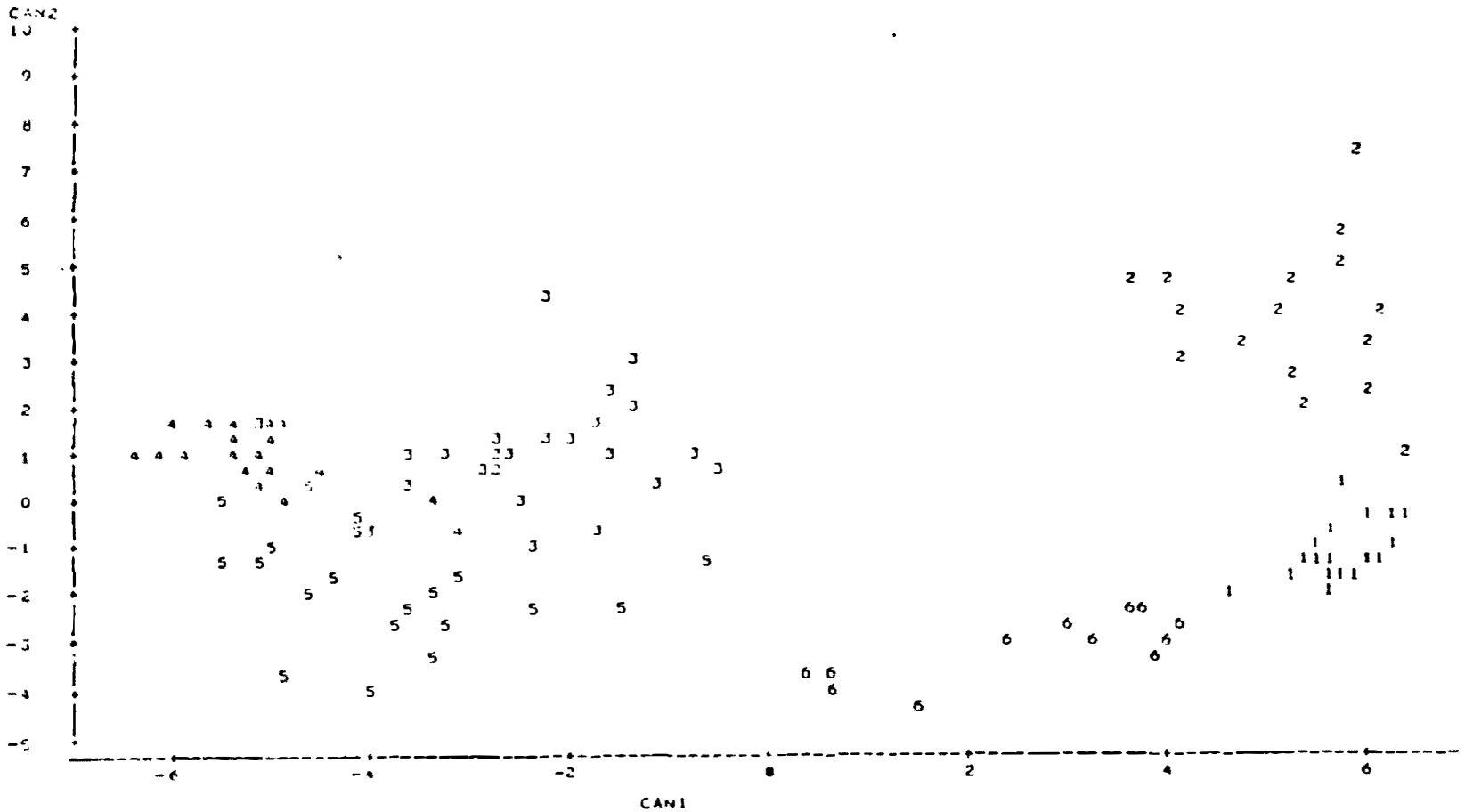

Figure 2. Cannonical representations of the first and second discriminant functions for habitat types in Custer State Park, South Dakota, 1985. 1 = mixed/grass forb, 2 = riparian, 3 = ponderosa pine/grass forb, 4 = ponderosa pine/no understory, 5 = steep rocky/ponderosa pine. 6 = steep rocky/grass forb. Can1 uses vegetation variables grass, forb, duff, bare ground, and canopy coverage. Can2 uses vegetation variables forb, rock, canopy coverage, and duff.

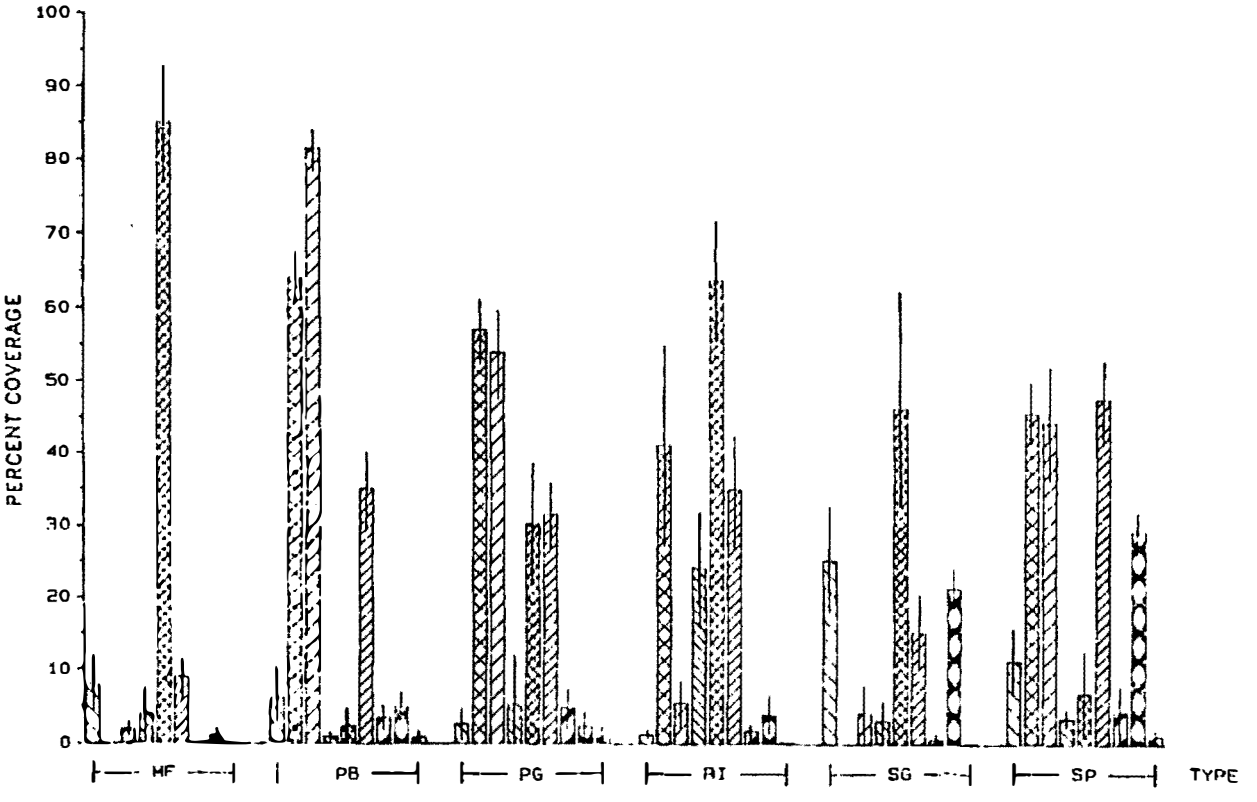

Figure 3. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges combined for each habitat type in Custer State Park, SD, 1985. MF = mixed/grass forb, PB = ponderosa pine/no understory, PG = ponderosa pine/grass forb, RI = riparian, SG = steep rocky/grass forb, SP = steep rocky/ponderosa pine.

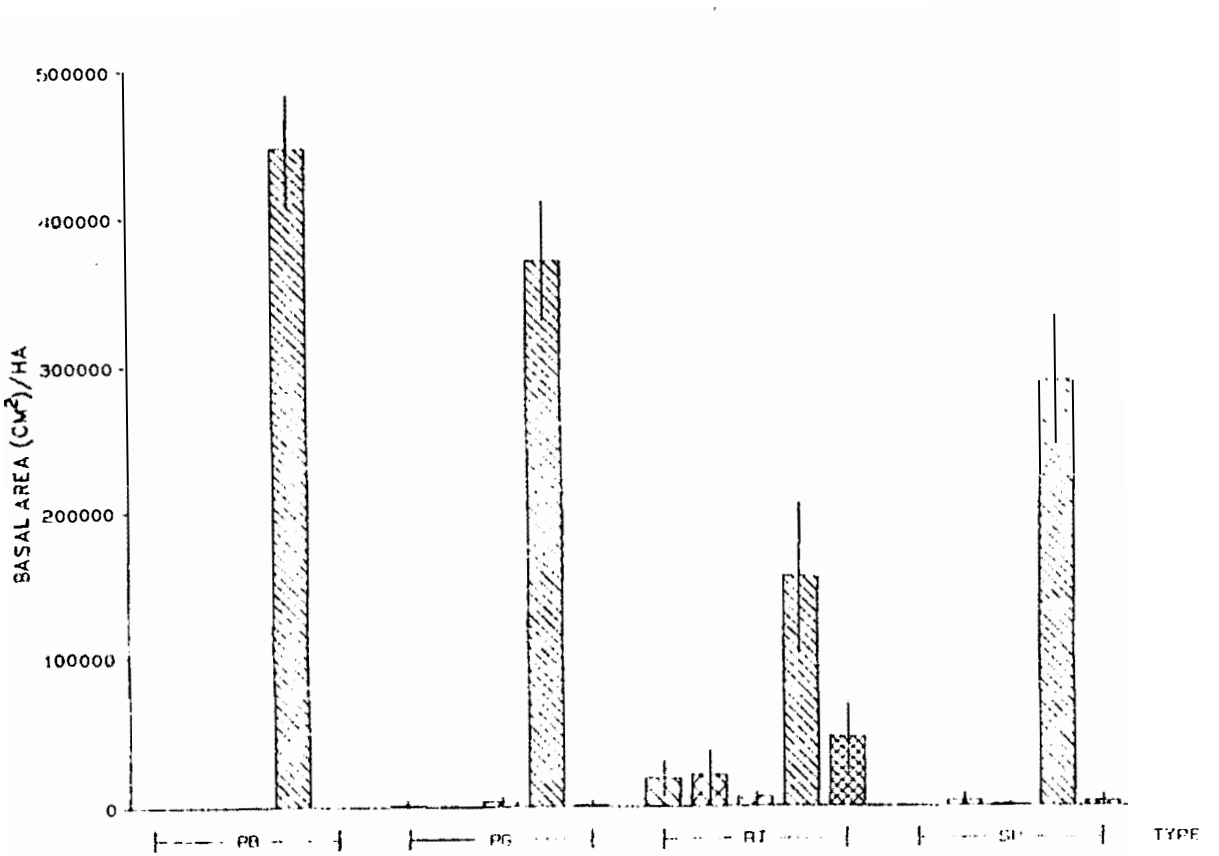

Figure 4. Mean (± se) of tree basal area/ha for all bighorn sheep ranges combined for each habitat type in Custer State Park, SD, 1985. PB = ponderosa pine/no understory, PG = ponderosa pine/grass forb, RI = riparian, SP = steep rocky/ponderosa p[illegible]

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

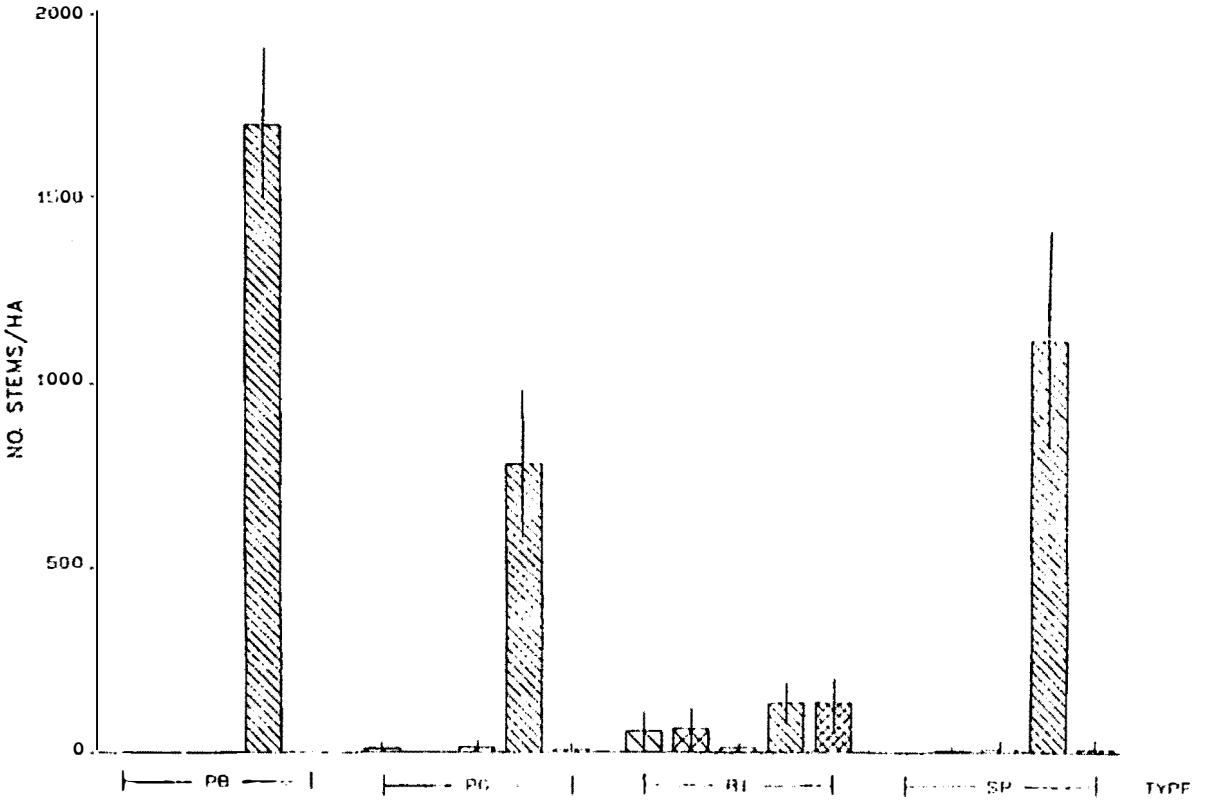

Figure 5. Mean (± se) of number of tree stems/ha for all Bighorn Sheep ranges combined for each habitat type in Custer State Park, SD, 1985. PB = ponderosa pine/bur oak understory, PG = ponderosa pine/grass forb, RI = riparian, SP = steep rocky/ponderosa pine.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

Although each habitat type was found to be similar in structure among all ranges, the proportions of area for each of these habitats were not similar. There were no consistent patterns among ewe ranges and ram ranges except for riparian (Table 3). The amount of riparian habitat was lower in ram ranges than ewe ranges ($F = 38.57$, $p < 0.0001$, $df = 12$). This difference may have been because the EE, WE, and part of the GC ranges included French Creek Canyon, the only extensive area of riparian habitat in any of the sheep ranges.

Habitat Utilization

Proportions of use and corresponding estimates of selection for or against each of the 7 habitat types, by the methods of Byers et al. (1984), for each sheep herd are contained in Appendix I. Both the WE and GC ewe herds selected for mixed grass/forb, while the EE herd used this habitat in proportion to its availability (Table 4). All 3 ewe herds selected against doghair ponderosa pine. The EE and WE herds also selected against ponderosa pine/no understory. The WE herd was the only herd that selected for riparian.

For the SW ram herd riparian, steep rocky/grass forb, and doghair ponderosa pine types were selected against while the other habitats were utilized in proportion to their availability. The SE ram herd

Table 3. Proportion and area (ha) of each habitat type found within each bighorn sheep herd home range from July through October, 1985, in Custer State Park, South Dakota.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	0.137 (66.11)	0.025 (27.76)	0.026 (18.34)	0.056 (35.63)	0.055 (61.34)
ponderosa pine/ no understory	0.289 (139.79)	0.359 (396.75)	0.254 (181.98)	0.498 (316.52)	0.178 (196.67)
ponderosa pine/ grass forb	0.243 (117.55)	0.103 (113.49)	0.166 (119.42)	0.206 (131.07)	0.306 (338.97)
riparian	0.039 (18.73)	0.032 (35.32)	0.025 (17.90)	0.009 (5.97)	0.008 (8.65)
steep rocky/ grass forb	0.022 (10.50)	0.020 (21.86)	0.009 (6.20)	0.054 (34.52)	0.021 (23.15)
steep rocky/ ponderosa pine	0.245 (118.58)	0.319 (352.47)	0.368 (264.09)	0.101 (64.34)	0.373 (412.68)
doghair ponderosa pine	0.026 (12.68)	0.142 (156.40)	0.153 (109.75)	0.075 (47.73)	0.060 (65.92)
Total home range size (ha)	493.95	1104.05	717.62	635.78	1107.28

Table 4. Selection for and against[1] habitat types by Rocky Mountain bighorn sheep herds in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	0	+	+	0	0
ponderosa pine/ no understory	-	-	0	-	0
ponderosa pine/ grass forb	0	0	0	+	0
riparian	0	-	0	-	-
steep rocky/ grass forb	0	0	0	0	-
steep rocky/ ponderosa pine	0	0	0	0	0
doghair ponderosa pine	-	-	-	-	-

[1] 0 indicates no selection
+ indicates selection for a habitat type
- indicates selection against a habitat type

likewise selected against doghair ponderosa pine and riparian but, in addition, selected against ponderosa pine/no understory, while selecting for ponderosa pine/grass forb habitat.

Pooling the 3 ewe herds and both ram herds resulted in a difference of habitat utilization than those found among individual sheep herds (Table 5). For the pooled ewe herds, both the mixed grass/forb and riparian habitats were selected for while doghair ponderosa pine and ponderosa pine/no understory were selected against. Doghair ponderosa pine and riparian were selected against by the pooled ram herds, while ponderosa pine/grass forb was selected for.

Activity Budgets

Feeding was the most frequent activity encountered for all herds except the SW ram herd (X^2 = 15.88, $p < 0.01$, df = 3, Table 6). Feeding was the second most frequent activity for the SW herd and was probably an artifact of small sample size. Standing was not a frequent activity for any herd. The remainder of the activities observed were divided between resting and moving and were similar among the herds (X^2 = 3.38, p = 0.4981, df = 4).

Resting areas for all herds (Table 7) were found most frequently in steep rocky/ponderosa pine habitat,

Table 5. Selection and avoidance of habitat types by pooled ram and ewe bighorn sheep herds in Custer State Park, SD, from July through October, 1985.

Habitat Type	pooled ewe herds	pooled ram herd
mixed grass/ forb	-	0
ponderosa pine/ no understory	-	0
ponderosa pine/ grass forb	0	+
riparian	+	-
steep rocky/ grass forb	0	0
steep rocky/ ponderosa pine	0	0
doghair ponderosa pine	-	-

[1] 0 indicates no selection
+ indicates selection for a habitat type
- indicates selection against a habitat type

Table 6. Proportion (no. of observations) of behavior categories for bighorn ram and ewe sheep herds in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Activity	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
Resting	0.247 (18)	0.180 (16)	0.151 (8)	0.206 (7)	0.500 (7)
Moving	0.151 (11)	0.180 (16)	0.208 (11)	0.382 (8)	0.214 (3)
Standing	0.068 (5)	0.067 (6)	0.151 (8)	0.029 (1)	--[a]
Feeding	0.534 (39)	0.573 (51)	0.491 (26)	0.529 (18)	0.286 (4)
Total Number Observations	73	89	53	34	14

[a] -- represents no observed occurrences.

Table 7. Relative frequency (no. observations) of resting activity by Rocky Mountain bighorn sheep herds for each habitat type in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	0.00 (0)	0.06 (1)	0.13 (1)	0.00 (0)	0.00 (0)
ponderosa pine/ no understory	0.11 (2)	0.06 (1)	0.25 (2)	0.14 (1)	0.29 (2)
ponderosa pine/ grass forb	0.28 (5)	0.06 (1)	0.25 (2)	0.57 (4)	0.14 (1)
riparian	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)
steep rocky/ grass forb	0.11 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
steep rocky/ ponderosa pine	0.50 (9)	0.75 (12)	0.38 (3)	0.29 (2)	0.57 (4)
doghair ponderosa pine	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)

except for the SE ram herd, which used ponderosa pine/grass forb ($X^2 = 13.04$, $p < 0.05$, $df = 6$). Utilization analyses revealed that only the WE ewe herd selected for steep rocky/ponderosa pine as resting sites (Table 8). Only doghair ponderosa pine was consistently selected against by all herds.

Feeding areas were less consistent among herds (Table 9), and included riparian, ponderosa pine/grass forb, and mixed grass/forb habitats as the most frequently used feeding habitats. The EE ewe herd spent most of its feeding time in ponderosa pine/grass forb but also utilized steep rocky/ponderosa pine and mixed grass/forb to a lesser extent. The WE ewe herd fed mostly in riparian and mixed grass/forb and, to a much lesser extent, in ponderosa pine/grass forb. The GC ewe herd fed most frequently in mixed grass/forb and also ponderosa pine/grass forb and riparian habitats. Only ponderosa pine/grass forb was used extensively for feeding by the SE ram herd while the SW ram herd used mixed grass/forb more frequently and, to a lesser extent, both ponderosa pine/grass forb and riparian, although again, this may only be an artifact due to small sample size. Selection of feeding areas, determined using the methods of Byers et al. (1984), generally followed trends found in frequency comparisons (Table 10). All herds

Table 8. Selection and avoidance[1] of habitat types used for resting sites by Rocky Mountain bighorn sheep herds in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	-	0	0	-	-
ponderosa pine/ no understory	0	-	0	0	0
ponderosa pine/ grass forb	0	0	0	0	0
riparian	-	0	-	-	0
steep rocky/ grass forb	0	-	-	-	0
steep rocky/ ponderosa pine	0	+	0	0	0
doghair ponderosa pine	-	-	-	-	-

[1] 0 indicates no selection
+ indicates selection for a habitat type
- indicates selection against a habitat type

Table 9. Relative frequency (no. observations) of feeding activity by Rocky Mountain bighorn sheep herds for each habitat type in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	0.26 (10)	0.33 (17)	0.35 (9)	0.17 (3)	0.50 (2)
ponderosa pine/ no understory	0.03 (1)	0.00 (0)	0.04 (1)	0.00 (0)	0.00 (0)
ponderosa pine/ grass forb	0.41 (16)	0.16 (8)	0.31 (8)	0.61 (11)	0.25 (1)
riparian	0.05 (2)	0.43 (22)	0.23 (6)	0.00 (0)	0.25 (1)
steep rocky/ grass forb	0.05 (2)	0.02 (1)	0.00 (0)	0.11 (2)	0.00 (0)
steep rocky/ ponderosa pine	0.21 (8)	0.06 (3)	0.08 (2)	0.11 (2)	0.00 (0)
doghair ponderosa pine	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)

Table 10. Selection and avoidance[1] of habitat types used for feeding by Rocky Mountain bighorn sheep herds in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	0	+	+	0	0
ponderosa pine/ no understory	-	-	-	-	-
ponderosa pine/ grass forb	0	0	0	+	0
riparian	0	+	0	-	0
steep rocky/ grass forb	0	0	-	0	-
steep rocky/ ponderosa pine	0	-	-	0	-
doghair ponderosa pine	-	-	-	-	-

[1] 0 indicates no selection
+ indicates selection for a habitat type
- indicates selection against a habitat type

selected against ponderosa pine/no understory and doghair ponderosa pine types as feeding habitats.

Distances from resting sites to escape terrain were mostly consistent among the herds, since the most frequent habitat used for resting also consisted of one type of escape terrain, steep rocky/ponderosa pine. Mean distances from these resting sites to escape terrain for all herds except the SE ram herd were less than 10 m. For the SE ram herd, which utilized ponderosa pine/grass forb most frequently for resting sites, the mean distance to escape terrain was 83 m.

Mean distances from feeding areas to escape terrain were more variable than those from resting sites, depending on which habitats were utilized most frequently for feeding (Table 11). Mean escape distances among the ewe herds were not significantly different ($F = 5.02$, $p = 0.0632$) among the habitats most frequently used for feeding. This was also true for the ram herds ($F = 1.58$, $p = 0.2431$), but the number of observations for the SW ram herd (2) were too small to make reliable comparisons. Distances to escape cover from most frequently utilized feeding habitats were significantly greater for rams than ewes ($F = 4.99$, $p = 0.0009$).

Table 11. Mean distance (no. observations) [group size] between locations of foraging sheep and escape terrain for all bighorn sheep herds for each habitat type in Custer State Park, SD, from July through October, 1985.

Distance (m) / Habitat Type	Sheep Herd: east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	73.6 (10) [14]	71.2 (17) [14]	40.4[a] (9) [13]	66.0 (3) [3]	99.0[a] (2) [1]
ponderosa pine/ no understory	15.0 (1) [11]	--[b]	40.0 (1) [2]	--	--
ponderosa pine/ grass forb	37.2[a] (16) [7]	36.9 (8) [12]	27.5 (8) [11]	80.6[a] (11) [5]	99.0 (1) [5]
riparian	22.5 (2) [6]	24.6[a] (22) [7]	30.8 (6) [7]	--	15.0 (1) [1]
steep rocky/ grass forb	5.0 (2) [5]	70.0 (1) [10]	--	20.0 (2) [3]	--
steep rocky/ ponderosa pine	6.3 (6) [6]	0.0 (3) [9]	0.0 (3) [11]	0.0 (2) [3]	--

[a] indicates most frequently utilized foraging habitat.
[b] -- indicates no observed occurrences.

DISCUSSION

Two predictions of the hypothesis that sexual segregation of bighorn sheep occur to reduce intersexual habitat competition (maintenance of home range fidelity between the sexes and similarity of physical characteristics for each habitat type among sheep ranges) were supported by the data in this study. Although the radio-tagged ram in the SW herd was observed on the WE range, no other members of the SW herd were found on the WE range. This ram was relatively young (4-years-old) and might not have completely established his home range, resulting in a lower ram herd affinity and increased wandering (Geist 1971). Otherwise, herd members maintained high fidelity to their respective range, and where ranges did overlap, temporal separation was maintained. Maintenance of separation during the summer and fall supported the argument that intersexual habitat competition occurred and was reduced by ram and ewes occupying separate ranges. If reduced habitat competition were not important, then greater spatial overlap of ranges would be expected, such as that found in the Ya Ha Tinda herd by Morgantini and Hudson (1981) during the winter, or that the sexes would have differential habitat requirements.

Similarity of physical characteristics for each

habitat type among sheep ranges demonstrated that establishment of each sheep range was not restricted to any particular types for any herd. This lended support to the assumption that the ranges were not qualitatively different, at least in terms of 3-dimensional structure. It also supported the assumption that ranges presently occupied by CSP bighorn herds were not established according to differential habitat preferences or requirements between sexes.

Although forage quality was found to differ between ram and ewe ranges in a study by Shank (1979), he suggested that these differences were too small to explain segregation based on these differences and found no basis for suggesting that different habitat requirements existed between sexes. However, both Morgantini and Hudson (1981) and Geist and Petocz (1977) reported differences in habitat occupation between rams and ewes during the winter for 2 different populations. In the herd studied by Geist and Petocz (1977), rams were found on areas with more grassy slopes, while ewes occupied steeper, more rocky terrain. Rams occupied more rocky and steeper terrain than ewes in the Ya Ha Tinda herd (Morgantini and Hudson 1981). If both sexes required similar habitats, then habitat occupation should have been similar between the sexes, whether they

segregated or not, and should have been consistent over the geographical range that bighorn sheep inhabit (Morgantini and Hudson 1981). Since habitats occupied by each sex were not consistent, these two studies support the conclusion that rams and ewes do not have different habitat requirements. Therefore, rams and ewes may be equally likely to establish seasonal ranges over similar habitat types and potentially compete with each other for resources within those ranges.

In order to demonstrate that competition for habitat resources occurred between the sexes, the prediction was made that habitat types were utilized with similar frequencies, between the sexes. However, utilization analyses for habitat types did not support this prediction for comparisons among the herds (Table 4). Although most types were utilized in proportion to their availability for each herd, when there was selection for or against a habitat type, types selected were inconsistent among the herds, except for doghair ponderosa pine.

Utilization analysis between sexes for pooled herds suggested differences of habitat utilization between rams and ewes (Table 5). However, since habitat utilization was different for each herd, regardless of sex, pooling was not considered justified to make

comparisons between sexes.

Simple comparison of habitat type utilization for all sheep locations may not be adequate in determining whether intersexual competition occurs or not, since all behavior categories were lumped for the utilization analyses. Competition may be critical for only a few resources, and since Geist (1971) noted that feeding areas and resting sites were important factors in determining sheep distribution, habitat utilization analyses for these two behavior categories would also be important in evaluating whether competition occurred between the sexes for these two resources.

Comparison of habitat utilization among the herds for feeding areas did not support the prediction that any habitat type selected for feeding areas would be similar among the herds (Table 8). Also, the analysis did not demonstrate that ewes consistently selected for any particular habitat type for feeding that were different from rams; thus, there was no indication that habitat requirements for feeding areas might be different between the sexes. Utilization of habitats for resting sites suggested that some types were not suitable for this behavior (Table 11), but lack of selection for any of the other habitat types did not support either similarity of selection among the herds or that there were intersexual

differences of habitat selection for resting sites.

One problem with using utilization analysis for establishing whether habitat competition occurred between sexes was that only the results of selection for or against a habitat type were useful to make comparisons. The test provided no information regarding differential frequency of use between habitat types, only whether a type was utilized more than, less than, or in proportion to its availability. Thus, no information could be obtained by comparing, among herds, types which were utilized according to proportion of their availability.

Another problem with using results of habitat utilization from this study for determining whether intersexual competition occurred or not is the small number of observations used to estimate habitat utilization. Byers et al. (1984) suggested that expected frequency of usage should be 5 or greater, in all categories, to insure adequate sample size for their utilization estimator. Expected frequencies of several habitat types for every sheep herd were less than 5, possibly leading to biased results, where there were not enough observations to establish whether selection actually existed or not (Table 12).

Table 12. Expected number of occurrences of use for each habitat type by Rocky Mountain bighorn sheep herds in Custer State Park, SD, from July through October, 1985.

	Sheep Herd				
Habitat Type	east end ewe herd	west end ewe herd	Grace Coolidge ewe herd	southeast ram herd	southwest ram herd
mixed grass/ forb	10	17	1	2	1
ponderosa pine/ no understory	21	6	13	17	2
ponderosa pine/ grass forb	17	9	8	7	3
riparian	3	3	1	0	0
steep rocky/ grass forb	2	2	0	2	0
steep rocky/ ponderosa pine	18	27	19	3	4
dogtail ponderosa pine	2	12	8	3	1

Comparison among herds of types used most frequently for resting and feeding provided some basis for supporting similarity of habitat use between the sexes. Although utilization analysis showed that only the WE ewe herd selected for steep rocky/ponderosa pine, this type was most frequently used as resting sites for all but the SE ram herd. This herd used steep rocky/ponderosa pine second to ponderosa pine/grass forb. This suggests that steep rocky/ponderosa pine was the most important habitat type for resting sites among CSP sheep herds.

While there was less consistency in most frequently used habitat types for feeding, riparian, mixed grass/forb, and ponderosa pine/grass forb were the most important types for the sheep herds (Table 9). There was no evidence for intersexual differences of types used for feeding as each ewe herd and each ram herd used a different type most frequently. This suggested no differences in habitat requirements between rams and ewes in those types most used for feeding. However, since only these 4 types were most frequently used by all of the sheep groups, then evidence of intersexual competition for feeding habitats can be suggested. This provided support for the hypothesis of segregation to reduce competition between the sexes and conformed to the

assumption that habitat types were used with similar frequencies by the sexes.

Inconsistencies of habitat types used for feeding by ram and ewe herds may have been influenced by size of groups within herds. Risenhoover and Bailey (1985) found group size and distance to escape terrain important in predicting foraging efficiency and distribution of bighorn sheep. Small groups (1-5 individuals) were less efficient than medium (6-10 individuals) and large (>10 individuals) groups. Small groups were also rarely found foraging very far from escape terrain, while large groups were found to forage at greater than expected distances from escape terrain. Thus, group size may be important in determining how efficiently bighorn sheep are able to exploit available foraging areas. If group size is too small, then foraging areas may be restricted to areas relatively close to escape terrain. Since a maximum of 7 sheep comprised the SE ram herd and the SW ram herd consisted of 4 individuals, while ewe herd sizes were much larger (Table 9), utilization of feeding areas may have been restricted for the ram herds. However, rams were found to forage much farther from escape terrain than ewes, even though average group size of rams was considered small. Thus, rams were considered not excluded from foraging areas located at relatively great

distances from escape terrain because of small group size. The failure of predicting group size and distance to escape terrain in CSP rams and may have caused inconsistencies in utilization of those types used for feeding.

Results for habitat types used for feeding among the herds were especially important since forage competition is probably the most important form of habitat competition between the sexes, and since reproductive fitness of females is considered to be most dependent on foraging efficiency (Clutton-Brock et al. 1982). The results from this study supported the predictions that the sexes occupy home ranges that share similar physical characteristics for each habitat type and that spatial and temporal fidelity of home range occupation is maintained. The data also suggested that both sexes utilized habitat types with similar frequencies, but this conclusion is tentative at best, given the paucity of data for the ram herds. The data also led to the conclusion that rams and ewes do not exhibit differential habitat requirements, a result previously reached by Shank (1979). On the other hand, Clutton-Brock et al. (1983) concluded that red deer (Cervus elaphus) sexes did segregate according to differences in habitat preferences suggesting that

failure to support the hypothesis proposed by Geist and Petocz (1977) using data from CSP bighorn sheep may be unique only to this study.

Although the hypothesis of segregation to minimize habitat competition between rams and ewes (Geist and Petocz 1977) can explain maintenance of sexual segregation year-round, it does not preclude separation in order to reduce agonistic interactions among rams and ewes when reproduction is not possible. Geist (1971) described the forms of each age and sex in a social context. Basically, older rams (8 years and older) are the mature forms of bighorn sheep. Mature in this case means physical, psychological, and social maturation. Older rams regard all smaller rams, adult ewes, yearlings, and juveniles merely as undeveloped rams and treat them as such (Geist 1971). Estrous ewes and subordinate rams react to aggressive advances by larger males with a set of specific behavior patterns which allows the aggressor to express its dominance. Nonestrous females and lambs simply withdraw and leave the intentions of the aggressive male incomplete. These encounters may result in the aggressor (male) chasing the recipient (female) for some distance thus increasing energy expenditures for ewes and lambs. Geist (1971) has also documented that rams spar for dominance year-round

and interprets this to mean that rams may compete for dominance, not females. Thus, males that have become dominant in ewe herds can be detrimentally stressful to pregnant or lactating ewes by remaining in ewe herds and continually asserting their dominance. Younger rams (3-5 years old) leave female herds only after becoming dominant to all members of their herd, then join ram herds for the duration of their lives (Geist 1971). Any further social interactions with nonestrous ewes is meaningless for these dispersing rams. Further dominance can only be attained by interactions with larger males.

It is suggested that rams may segregate from ewes in order to reduce agonistic behaviors between the sex groups. By explaining sexual segregation in bighorn sheep in this manner, segregation can be maintained during the nonbreeding time of the year without invoking altruistic behaviors on the part of rams, where rams occupy poor quality ranges in order that ewe herds may occupy higher quality ranges. It would also explain inconsistencies of habitat utilization for feeding and resting sites found between the herds in this study by the fact that these inconsistencies would become unimportant. The other two assumptions, home range fidelity and similarity of habitat types within the ranges of both sexes, would follow from maintaining

segregation in order to reduce agonistic interactions between rams and ewes.

Critical tests to discriminate among the hypotheses which explain segregation are still needed as this study is inadequate to do this, or even fully support the hypothesis of reduced habitat competition. Repeated studies as outlined here are needed to determine any patterns of consistent distribution and habitat utilization across different bighorn sheep herds. Concurrent data to establish forage quality and/or quantity differences, between the sexes, are needed for different herds. Also, studies to decide the importance of ram-ewe social interactions during the breeding and nonbreeding seasons would be necessary to determine whether energy expenditures from these encounters would be great enough to warrant them as an explanation for sexual segregation. Regardless of which hypothesis is most fully supported, the accepted explanation should be adequate to completely explain sexual segregation found in Rocky Mountain bighorn sheep and, probably, all of the ungulates.

MANAGEMENT RECOMMENDATIONS

The behavior and habitat utilization of the CSP bighorn sheep population were found to be similar to other Rocky Mountain bighorn sheep herds. Since ram and ewe herds maintained spatial segregation throughout the nonbreeding portion of the year, it is concluded that a need for areas large enough to support separate ram and ewe ranges is necessary for maintenance of a bighorn population. Herd sizes would depend on the area of available habitat for each herd. Ewe herds apparently require rugged terrain (ie. escape cover) closer to foraging areas than rams did. Thus, when considering habitats for bighorn sheep, areas which might appear as suitable foraging sites may not be utilized and could not be included as bighorn sheep habitat. Habitat vegetation types may not need to be similar for ram and ewe ranges, but this cannot be considered conclusive from this study.

CSP rams were found to form 3 distinct herds where the herds were not observed to exchange members during the summer and fall. Since hunting within CSP is allowed, and rams are taken irrespective of herd membership, numbers of each ram herd, rather than just the ram population, should be monitored carefully to insure that one herd is not accidentally eliminated. In the event one herd was, one range of bighorn sheep

habitat would be effectively deleted from the CSP herd until individuals unfamiliar with that range learned to use it.

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APPENDIX I

Table A1. Occurrence of habitat occupation by the east end ewe herd in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	66.12	10	0.139	0.137	$0.029 \leq p_1 \leq 0.249$
ponderosa pine/ no understory	139.79	5	0.069	0.289[a]	$0.000 \leq p_2 \leq 0.150$
ponderosa pine/ grass forb	117.55	24	0.333	0.243	$0.184 \leq p_3 \leq 0.483$
riparian	18.73	2	0.028	0.039	$0.000 \leq p_4 \leq 0.080$
steep rocky/ grass forb	10.50	4	0.056	0.022	$0.000 \leq p_5 \leq 0.128$
steep rocky/ ponderosa pine	118.58	27	0.375	0.245	$0.222 \leq p_6 \leq 0.528$
doghair ponderosa pine	12.68	0	0.000	0.026[a]	$0.000 \leq p_7 \leq 0.000$
Totals	483.95	72			

[a] indicates selection against a habitat type at the 0.05 significance level.

Table A2. Occurrence of habitat occupation by the west end ewe herd in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	27.76	17	0.196	0.025[a]	$0.082 \leq p_1 \leq 0.313$
ponderosa pine/ no understory	396.75	6	0.070	0.359[b]	$0.000 \leq p_2 \leq 0.144$
ponderosa pine/ grass forb	113.49	11	0.128	0.103	$0.031 \leq p_3 \leq 0.225$
riparian	35.32	25	0.291	0.039[a]	$0.159 \leq p_4 \leq 0.422$
steep rocky/ grass forb	21.86	2	0.023	0.020	$0.000 \leq p_5 \leq 0.067$
steep rocky/ ponderosa pine	352.47	25	0.291	0.319	$0.159 \leq p_6 \leq 0.422$
doghair ponderosa pine	156.40	0	0.000	0.142[b]	$0.000 \leq p_7 \leq 0.000$
Totals	1104.05	86			

[a] indicates selection for a habitat type at the 0.05 significance level.
[b] indicates selection against a habitat type at the 0.05 significance level.

Table A3. Occurrence of habitat occupation by the Grace Coolidge ewe herd in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	18.34	12	0.235	0.026[a]	$0.076 \leq p_1 \leq 0.395$
ponderosa pine/ no understory	181.98	10	0.196	0.254	$0.047 \leq p_2 \leq 0.346$
ponderosa pine/ grass forb	119.42	9	0.176	0.166	$0.033 \leq p_3 \leq 0.320$
riparian	17.90	6	0.118	0.025	$0.000 \leq p_4 \leq 0.239$
steep rocky/ grass forb	6.20	0	0.000	0.009	$0.000 \leq p_5 \leq 0.000$
steep rocky/ ponderosa pine	264.09	14	0.275	0.368	$0.106 \leq p_6 \leq 0.443$
doghair ponderosa pine	109.75	0	0.000	0.153[b]	$0.000 \leq p_7 \leq 0.000$
Totals	535.800	51			

[a] indicates selection for a habitat type at the 0.05 significance level.
[b] indicates selection against a habitat type at the 0.05 significance level.

Table A4. Occurrence of habitat occupation by the southeast ram herd in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	35.63	3	0.088	0.056	$0.000 \leq p_1 \leq 0.219$
ponderosa pine/ no understory	316.52	4	0.118	0.498[a]	$0.000 \leq p_2 \leq 0.266$
ponderosa pine/ grass forb	131.07	20	0.588	0.206[b]	$0.361 \leq p_3 \leq 0.815$
riparian	5.97	0	0.000	0.009[a]	$0.000 \leq p_4 \leq 0.000$
steep rocky/ grass forb	34.52	2	0.059	0.054	$0.000 \leq p_5 \leq 0.167$
steep rocky/ ponderosa pine	64.34	5	0.147	0.101	$0.000 \leq p_6 \leq 0.310$
doghair ponderosa pine	47.73	0	0.000	0.075[a]	$0.000 \leq p_7 \leq 0.000$
Totals	480.67	34			

[a] indicates selection against a habitat type at the 0.05 significance level.
[b] indicates selection for a habitat type at the 0.05 significance level.

Table A5. Occurrence of habitat occupation by the southwest ram herd in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	61.34	1	0.100	0.055	$0.000 \leq p_1 \leq 0.355$
ponderosa pine/ no understory	196.57	3	0.300	0.178	$0.000 \leq p_2 \leq 0.690$
ponderosa pine/ grass forb	338.97	1	0.100	0.306	$0.000 \leq p_3 \leq 0.355$
riparian	8.65	0	0.000	0.008[a]	$0.000 \leq p_4 \leq 0.000$
steep rocky/ grass forb	23.15	0	0.000	0.021[a]	$0.000 \leq p_5 \leq 0.000$
steep rocky/ ponderosa pine	412.68	5	0.500	0.373	$0.075 \leq p_6 \leq 0.925$
deghair ponderosa pine	65.92	0	0.000	0.060[a]	$0.000 \leq p_7 \leq 0.000$
Totals	1107.28	10			

[a] indicates selection against a habitat type at the 0.05 significance level.

Table A6. Occurrence of habitat occupation for pooled ewe herds in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (p_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	112.22	39	0.187	0.049[a]	$0.114 \leq p_1 \leq 0.259$
ponderosa pine/ no understory	718.52	21	0.100	0.312[b]	$0.045 \leq p_2 \leq 0.156$
ponderosa pine/ grass forb	350.46	44	0.211	0.152	$0.135 \leq p_3 \leq 0.286$
riparian	71.95	33	0.158	0.031[a]	$0.090 \leq p_4 \leq 0.226$
steep rocky/ grass forb	36.56	6	0.029	0.017	$0.000 \leq p_5 \leq 0.060$
steep rocky/ ponderosa pine	735.14	66	0.316	0.319	$0.229 \leq p_6 \leq 0.402$
deghair ponderosa pine	278.83	0	0.000	0.121[b]	$0.000 \leq p_7 \leq 0.000$
Totals	2305.68	209			

[a] indicates selection for a habitat type at the 0.05 significance level.
[b] indicates selection against a habitat type at the 0.05 significance level.

Table A7. Occurrence of habitat occupation for pooled ram herds in Custer State Park, SD, from July through October, 1985.

Habitat Type	Total Area (ha)	No. Groups Observed	Actual Proportion of Usage (p_i)	Expected Proportion of Usage (P_{io})	Bonferroni Intervals for p_i
mixed grass/ forb	96.97	4	0.091	0.036	$0.000 \leq p_1 \leq 0.207$
ponderosa pine/ no understory	513.09	7	0.159	0.294	$0.011 \leq p_2 \leq 0.307$
ponderosa pine/ grass forb	470.04	21	0.477	0.270[a]	$0.275 \leq p_3 \leq 0.680$
riparian	14.62	0	0.000	0.008[b]	$0.025 \leq p_4 \leq 0.000$
steep rocky/ grass forb	57.67	2	0.045	0.033	$0.000 \leq p_5 \leq 0.130$
steep rocky/ ponderosa pine	477.02	10	0.227	0.274	$0.057 \leq p_6 \leq 0.397$
doghair ponderosa pine	113.65	0	0.000	0.065[a]	$0.000 \leq p_7 \leq 0.000$
Totals	1743.06	44			

[a] indicates selection for a habitat type at the 0.05 significance level.

[b] indicates selection against a habitat type at the 0.05 significance level.

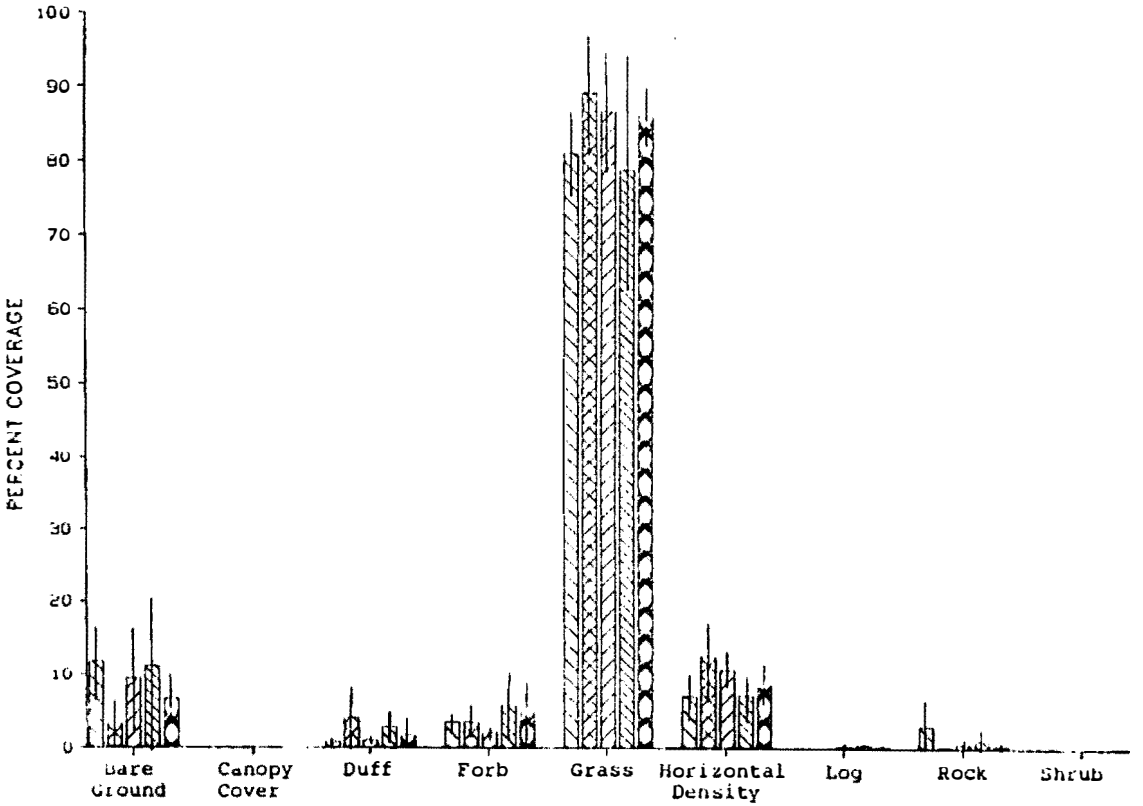

Figure A1. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for mixed grass/forb habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

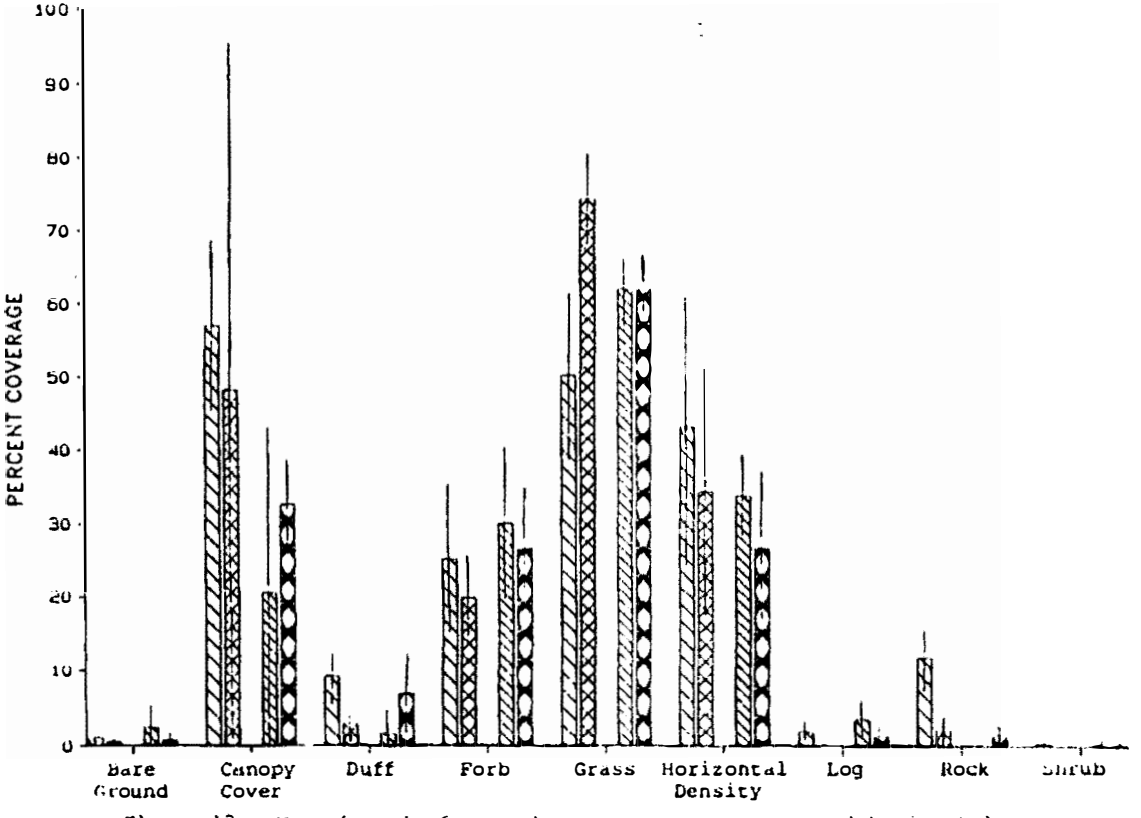

Figure A2. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for riparian habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

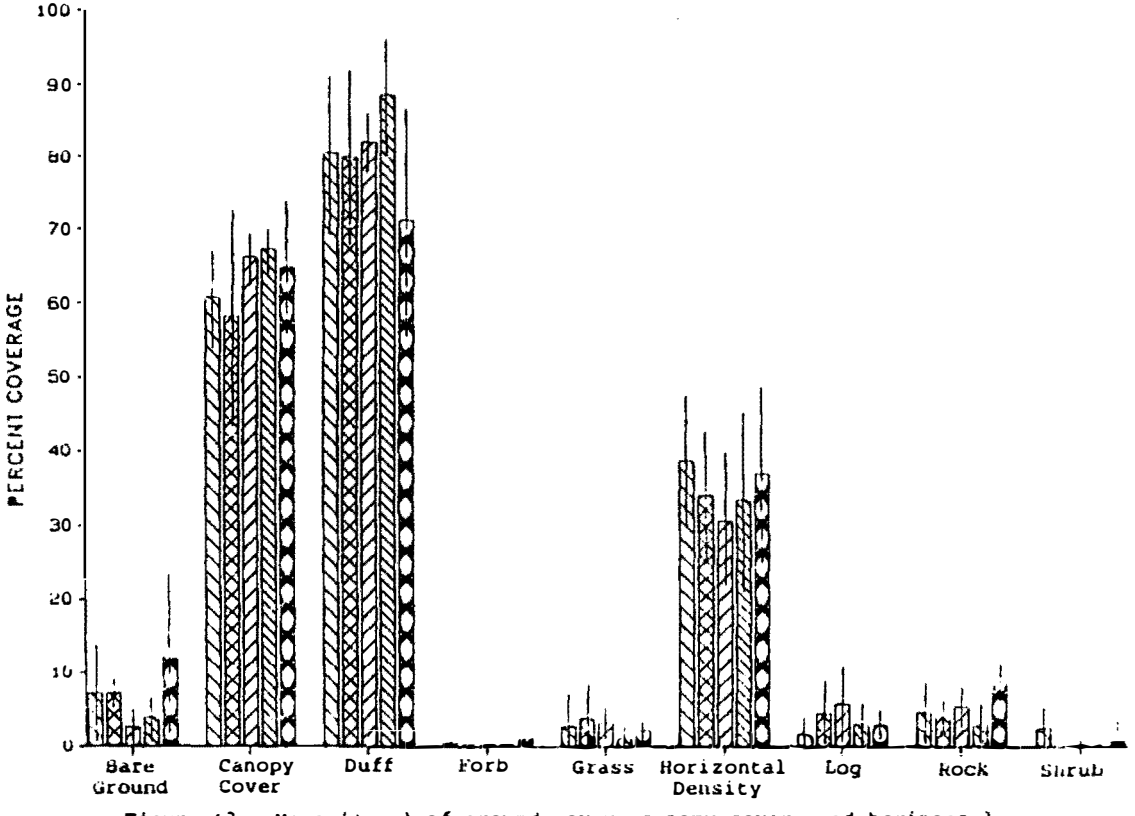

Figure A3. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for Ponderosa pine/no understory habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

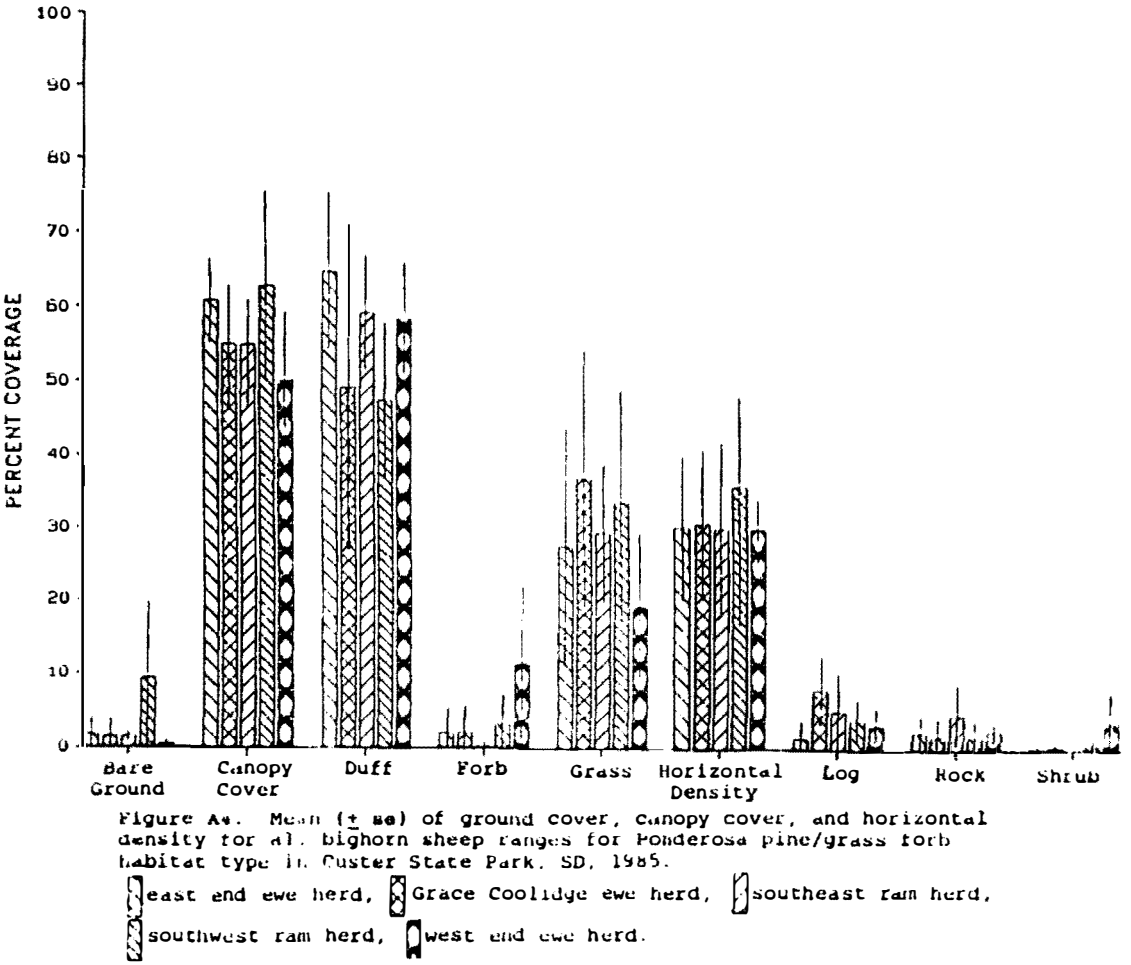

Figure A4. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for Ponderosa pine/grass forb habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

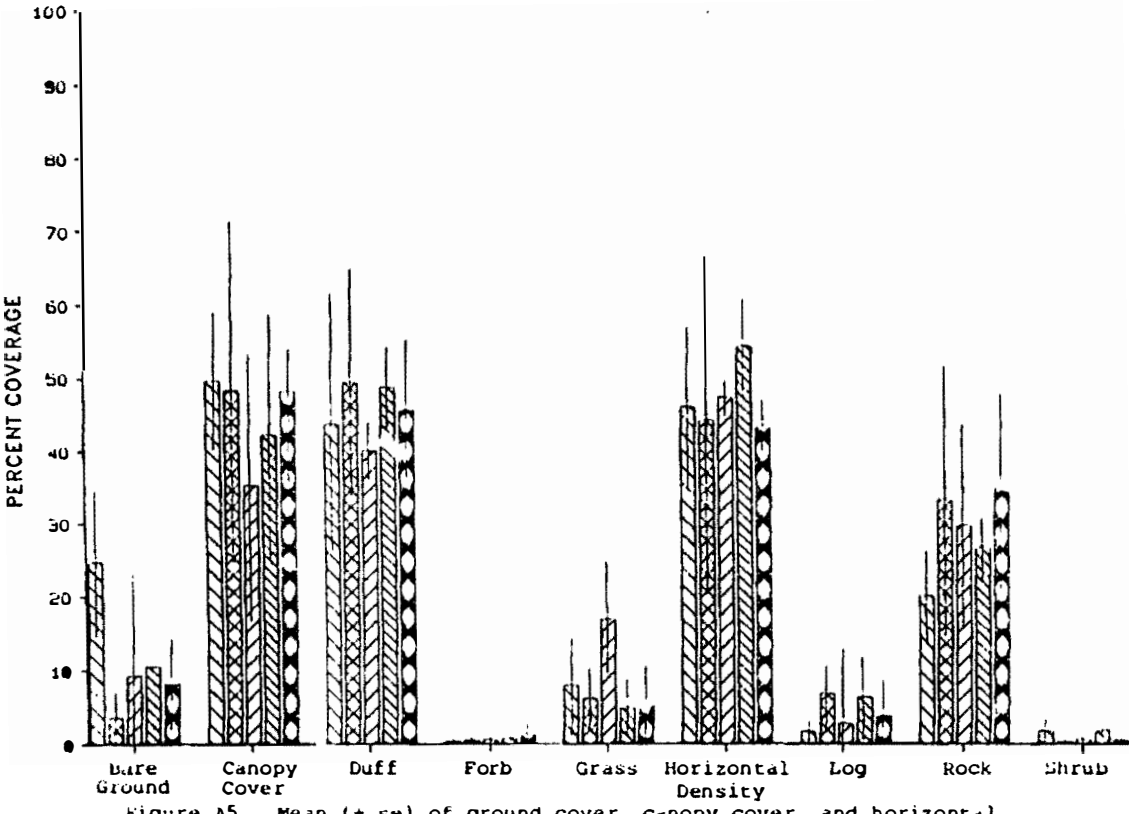

Figure A5. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for steep rocky/ponderosa pine habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

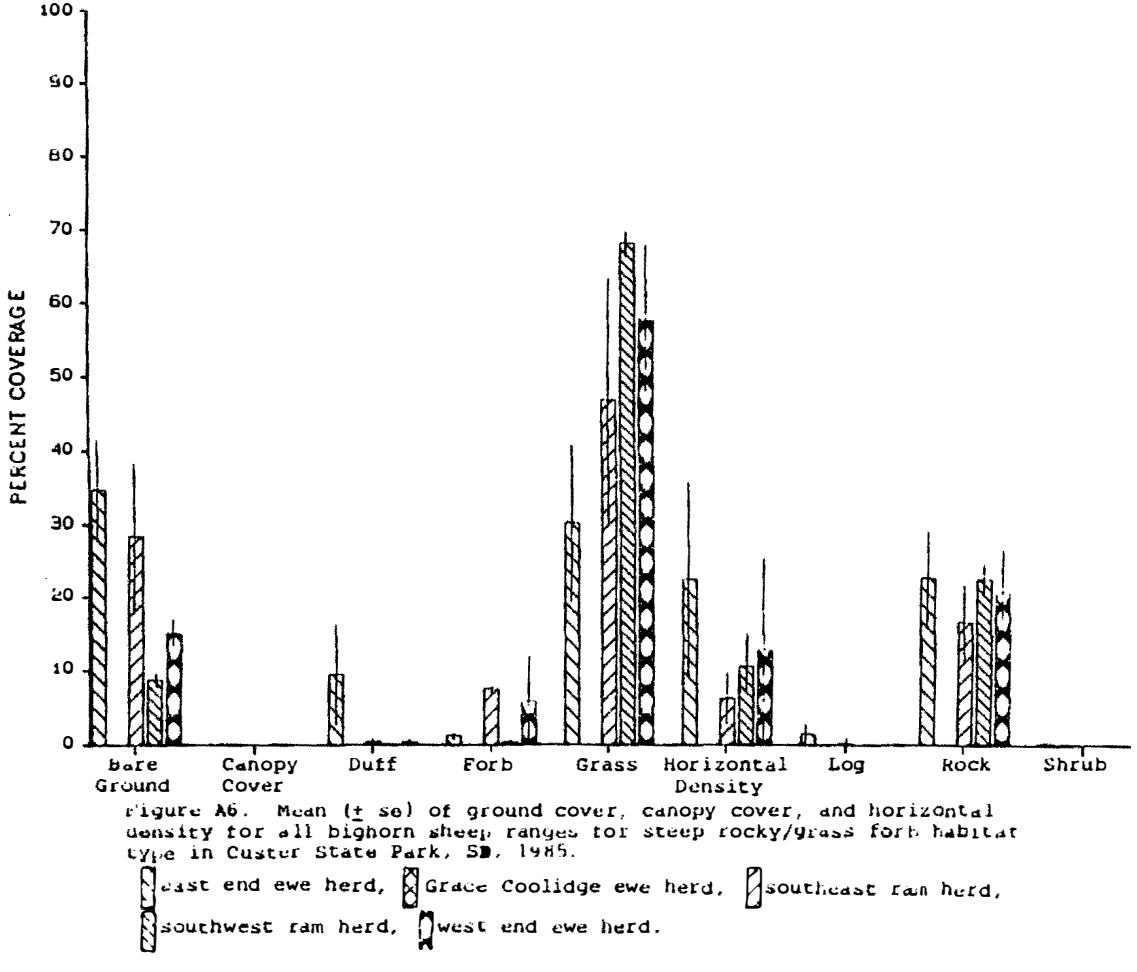

Figure A6. Mean (± se) of ground cover, canopy cover, and horizontal density for all bighorn sheep ranges for steep rocky/grass forb habitat type in Custer State Park, SD, 1985.

east end ewe herd, Grace Coolidge ewe herd, southeast ram herd, southwest ram herd, west end ewe herd.

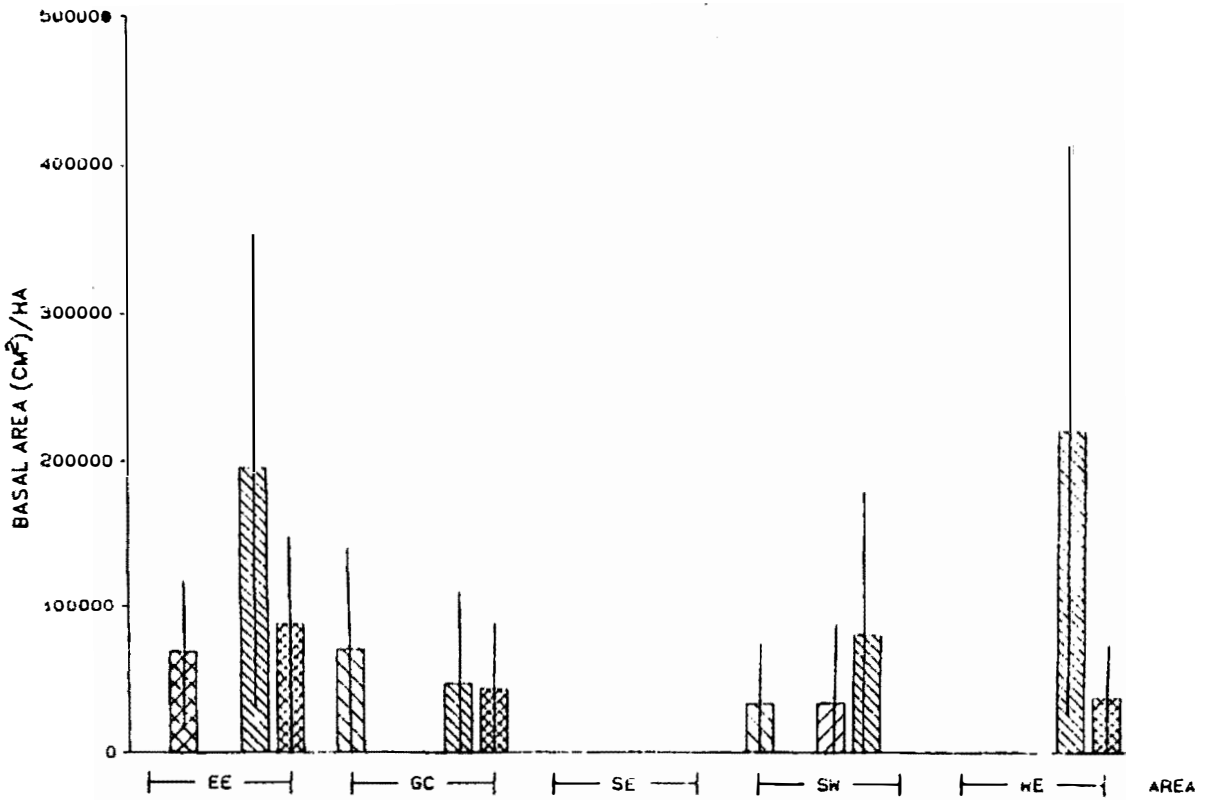

Figure A7. Mean (± se) of tree basal area/ha for all bighorn sheep ranges for riparian habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

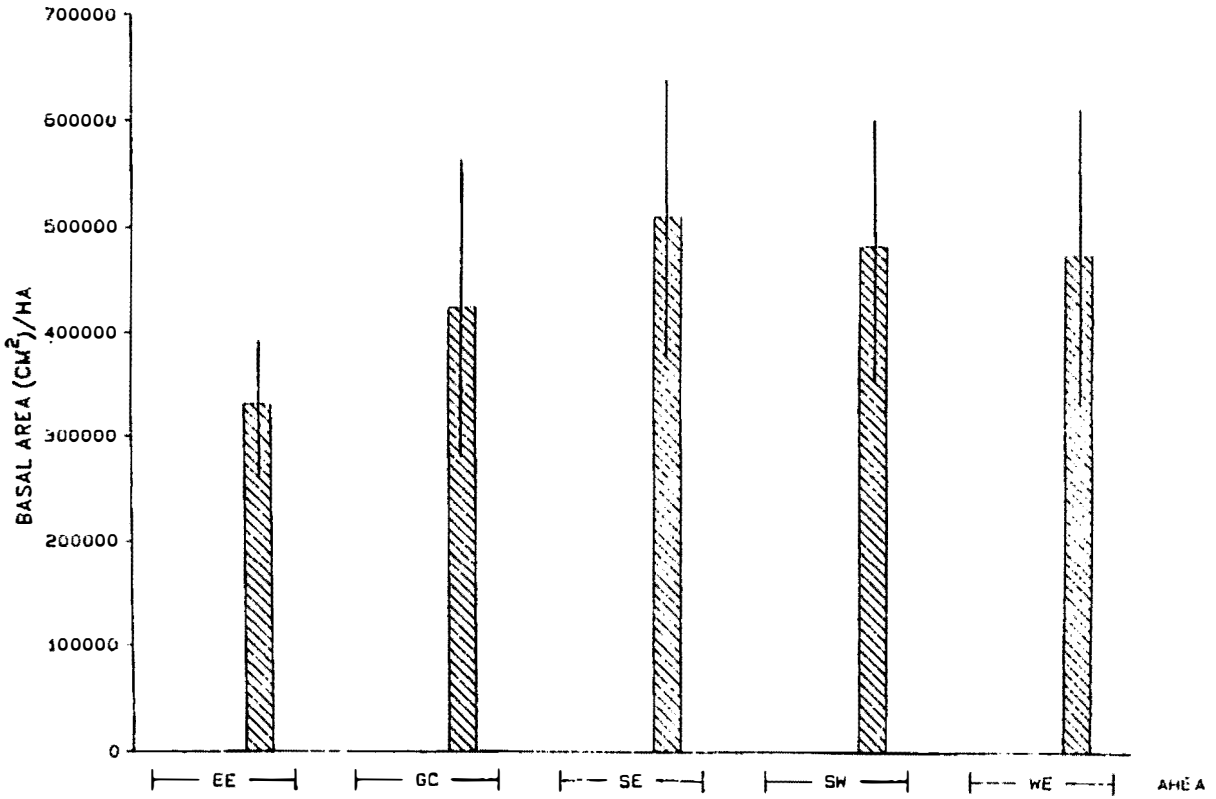

Figure A8. Mean (± se) of tree basal area/ha for all bighorn sheep ranges for Ponderosa pine/no understory habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

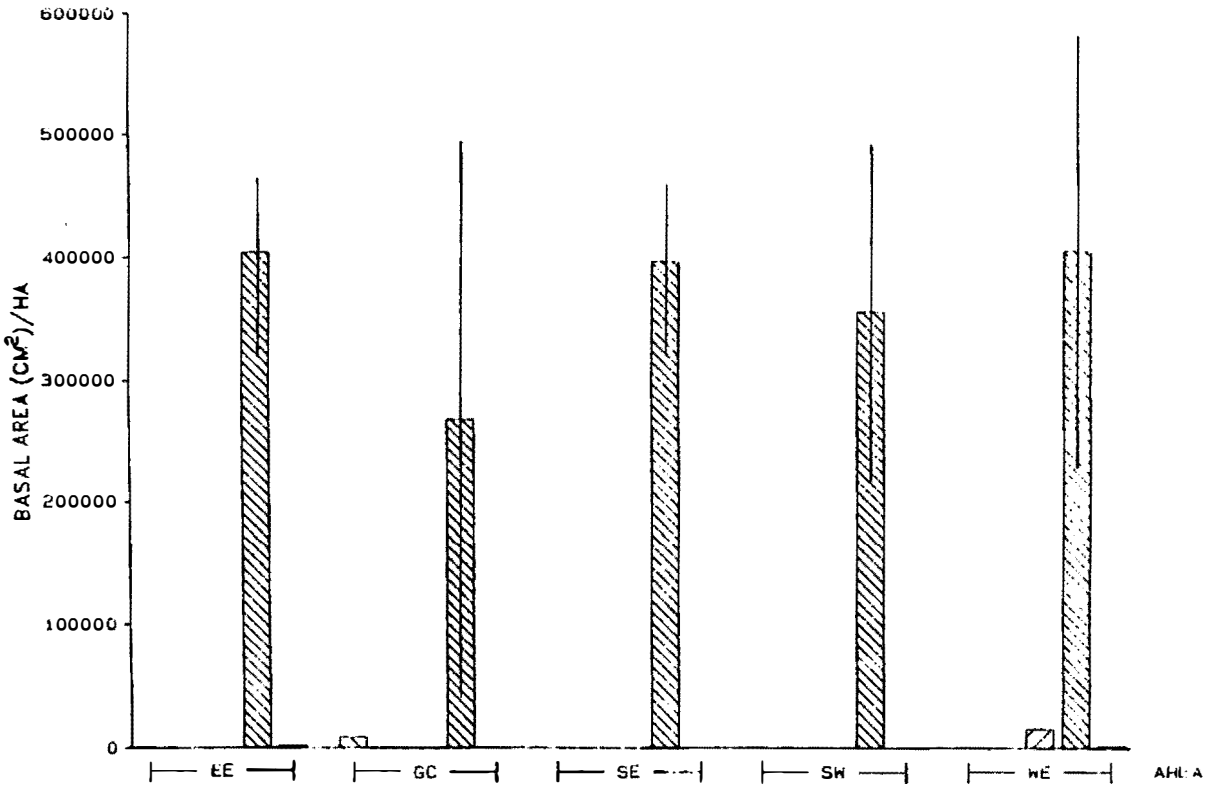

Figure A9. Mean (+ se) of tree basal area/ha for all bighorn sheep ranges for Ponderosa pine/grass forb habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

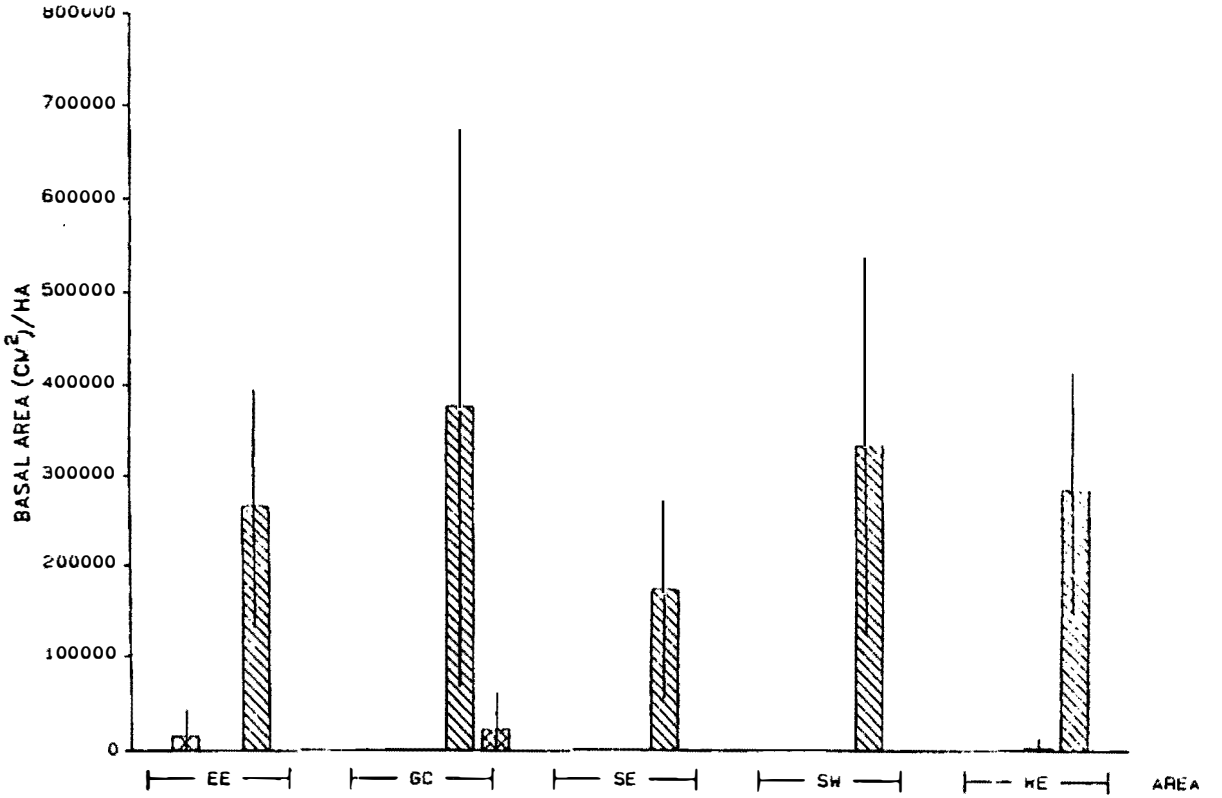

Figure A10. Mean (± se) of tree basal area/ha for all bighorn sheep ranges for steep rocky/ponderosa pine habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

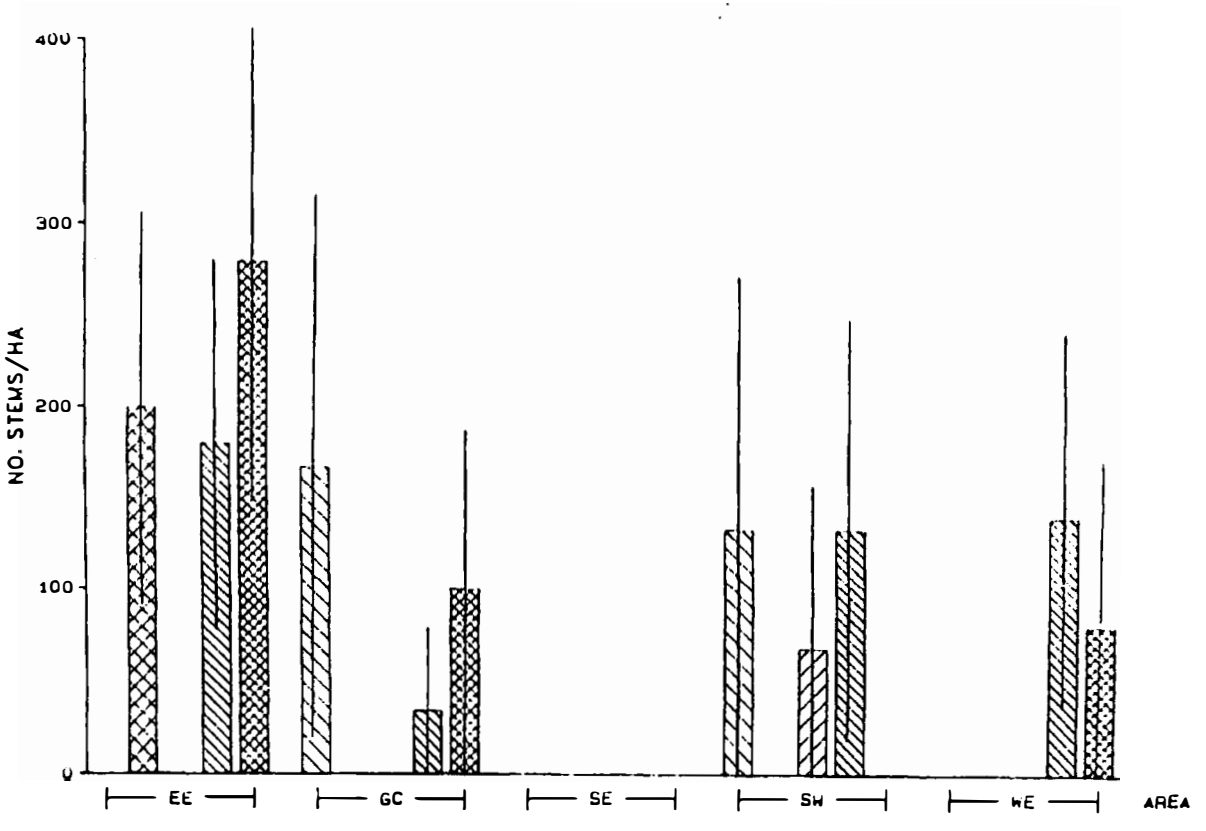

Figure A11. Mean (± se) of number of tree stems/ha for all bighorn sheep ranges for riparian habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

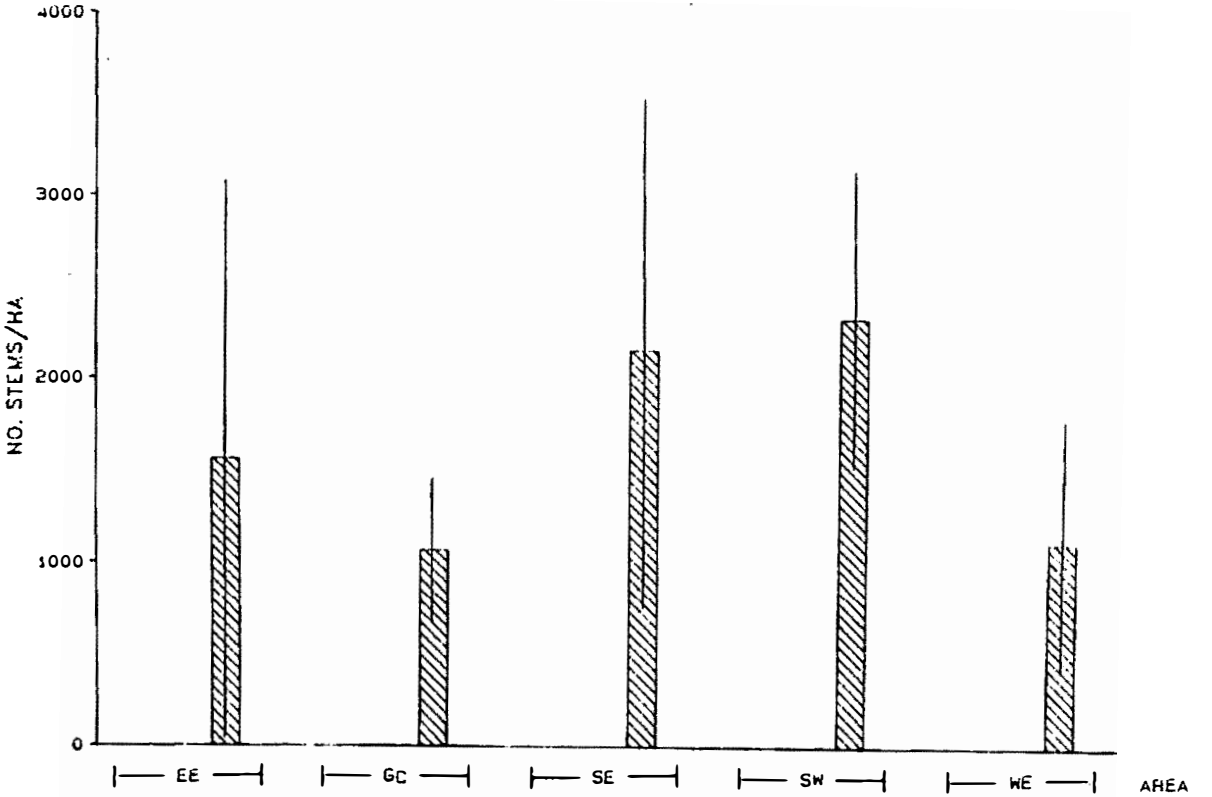

Figure A12. Mean (± se) of number of tree stems/ha for all bighorn sheep ranges for Ponderosa pine/no understory habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

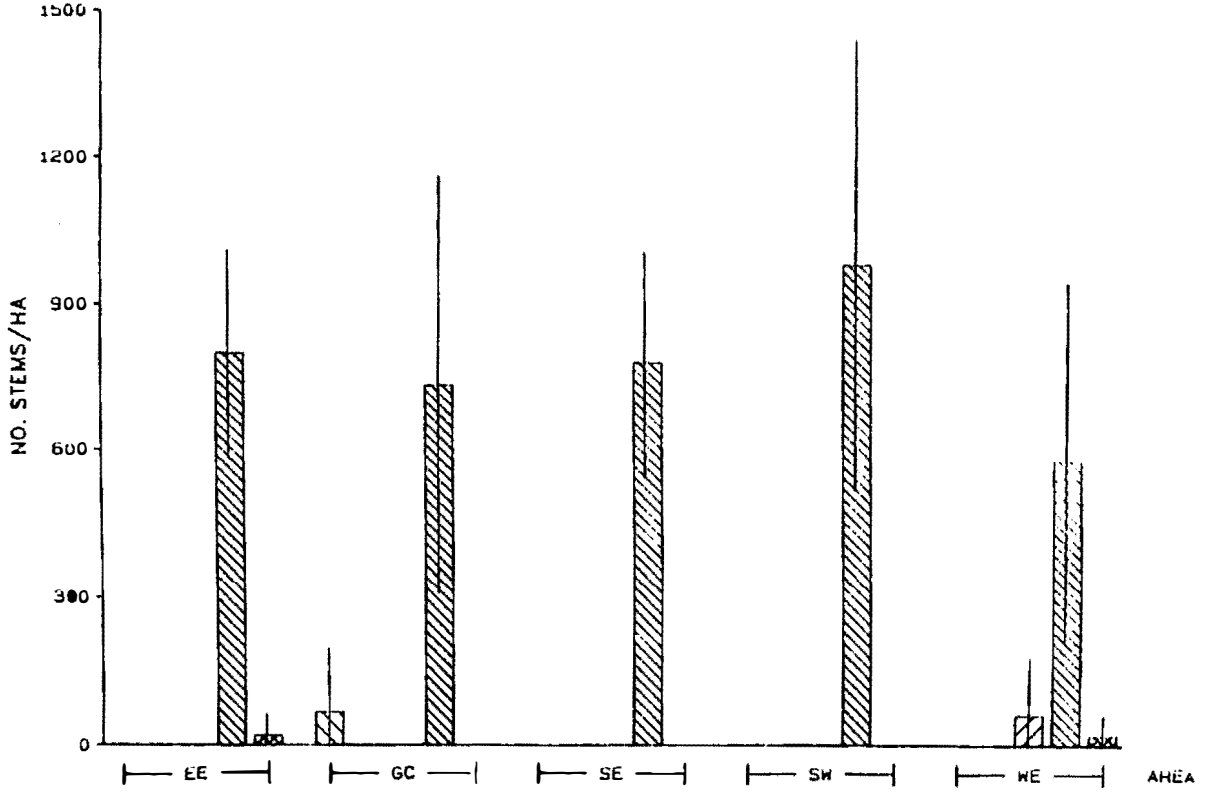

Figure A13. Mean (± se) of number of tree stems/ha for all bighorn sheep ranges for Ponderosa pine/grass forb habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.

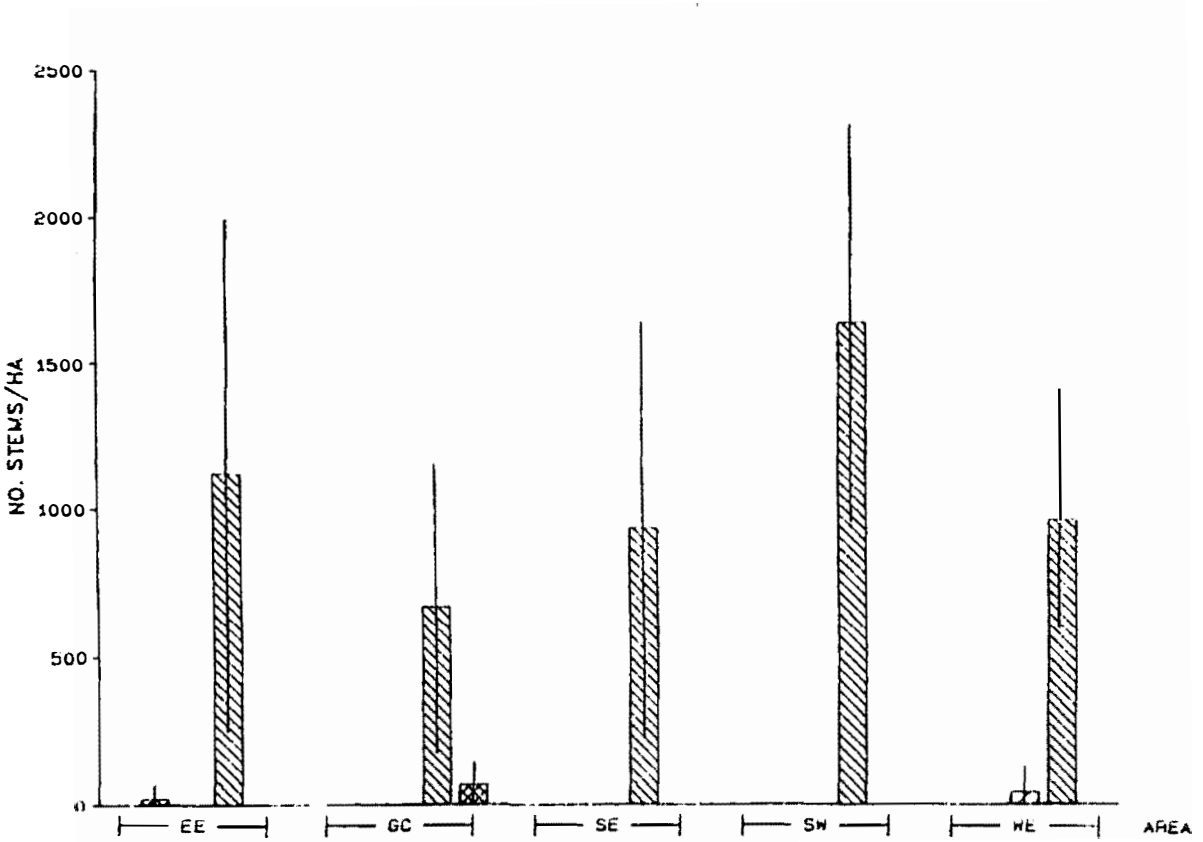

Figure A14. Mean (± se) of number of tree stems/ha for all bighorn sheep ranges for steep rocky/ponderosa pine/grass forb habitat type in Custer State Park, SD, 1985. EE = east end ewe herd, GC = Grace Coolidge ewe herd, SE = southeast ram herd, SW = southwest ram herd, WE = west end ewe herd.

Pinus ponderosa Quercus macrocarpa Betula papiferous

Populus tremuloides Miscellaneous species.