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Seasonal Variation in California Bighorn Ram (*Ovis canadensis californiana*) Habitat Use and Group Size

Abstract

Seasonal changes in bighorn sheep (*Ovis canadensis*) habitat use and social systems can create profound management challenges. We studied spring-summer distribution, habitat use, and group size of California bighorn rams on Poker Jim Ridge, Oregon. Ram groups were observed during April-August 1990. Herd range was smaller in spring (24.4 km^2) than summer (74.5 km^2). Ram groups were closer to escape terrain ($\underline{P} < 0.001$), farther from water ($\underline{P} < 0.001$), on gentler slopes ($\underline{P} = 0.01$) and at higher elevations ($\underline{P} < 0.001$) in spring. Distance to escape terrain and distance to water were significant main effects differentiating spring and summer habitat use ($\underline{P} < 0.001$). Ram group size varied by month ($\underline{P} < 0.001$), with groups in July-August smaller than those in April-June ($\underline{P} < 0.01$). Seasonal changes in ram distribution appeared to be associated with changing habitat conditions, particularly water availability. Small group sizes in late summer probably reflected resource limitations, and occurred in spite of use of less secure habitats during this period. Managers of bighorn sheep populations should consider the unique requirements of their populations under a variety of environmental conditions, and provide adequate protection to sustain seasonal shifts in distribution.

Introduction

Habitat quality in arid ecosystems can vary greatly between seasons, and is largely determined by precipitation regimens that control forage and water availability (Beatley 1974, Douglas and Leslie 1986, Wehausen et al. 1987). Numerous studies have shown that seasonal shifts in bighorn sheep distribution are related to changing habitat conditions (e.g., Welles and Welles 1961, Shannon et al. 1975, Leslie and Douglas 1979, Krausman and Leopold 1986, Krausman et al. 1989). These shifts presumably increase fitness by satisfying requirements for forage, water, thermal protection, escape cover, and areas for bedding, lambing and rutting (Shannon et al. 1975, Wilson et al. 1980, Tilton and Willard 1982). Bighorn sheep generally select open areas providing good visibility, adequate forage and access to escape terrain (Buechner 1960, Geist 1971, Risenhoover and Bailey 1985, Wakelyn 1987). During dry seasons or droughts, however, water availability may be a more important determinant of habitat selection (Welles and Welles 1961, Leslie and Douglas 1979). Sex-specific differences in habitat requirements (Blood 1963, Woolf et al. 1970, Geist 1971, Geist and Petocz 1977, Leslie and Douglas 1979, Morgantini and Hudson 1981, Gionfriddo and Krausman 1986, Krausman et al. 1989, Bleich et al. 1997) can result in different responses to seasonal changes in habitat condition between rams and ewes.

Bighorn sheep group sizes also reflect changing habitat conditions. Sheep may form smaller groups when resources are limited, thus avoiding resource depletion (Leslie and Douglas 1979, Berger 1979). Group size may also be a function of vegetative and physiographic structure; the formation of large groups enhances predator surveillance, allowing sheep to use habitats farther from escape terrain or with decreased visibility (Risenhoover and Bailey 1985, Warrick and Krausman 1987, Krausman et al. 1989).

Our objective was to describe seasonal shifts in bighorn ram distribution in relation to use of physiographic and vegetative habitat components. We also examined trends in group size over time, and hypothesized that group size would decrease during late summer in response to declining resources.

Study Area

The study was conducted on Poker Jim Ridge (PJR) (42°N, 119°W), a fault block mountain that comprised 89 km^2 of the northern portion of Hart Mountain National Antelope Refuge in Lake County, southeastern Oregon. The main axis of the ridge was oriented north-south. The west side rose precipitously from the Warner Valley (1,366 m) to a maximum elevation of 1,961 m. The top of PJR was a rolling plateau ≤2 km wide. The east side sloped gradually down to the Catlow

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Valley (1,555 m). Yearly precipitation averaged 27.0 cm, with the majority occurring as winter and spring snows. Water was available only in small ephemeral pools and two more reliable sources: Rock Creek, in the Catlow Valley ≥5 km east of the rim of PJR, and Petroglyph Lake, on the south end of PJR 1 km from the rim. Nineteen-ninety was a relatively dry year (19.0 cm precipitation) and Rock Creek was dry by mid-August. Vegetation was typical of the shrub-steppe communities described by Franklin and Dyrness (1973), which include sagebrush (*Artemisia tridentata*)-bunchgrass associations and stands of western juniper (*Juniperus occidentalis*). Forty-six adult and subadult rams ≥2 yr-old occupied PJR during 1990; a population of ewes, lambs and yearlings occupied the range for part of the year, but migrated elsewhere June-September (Payer 1992).

Methods and Materials

Bighorn ram groups were defined as groups consisting of adult and subadult males only. Ram group size and habitat use were assessed during 7 April to 31 August 1990 using direct observations of animals from 4 predetermined, non-overlapping routes. Each route was traveled 1 day per week. Ram group locations were plotted on U.S. Geological Survey 7.5-minute series topographic maps (1:24,000). We used the maps to measure elevation, slope (%), aspect (north, east, south, or west, corresponding to 315°-44°, 45°-134°, 135°-224° and 225°-314°, respectively), distance to water (= $[x^2 + y^2]^{0.5}$, where x = horizontal distance and y = vertical distance, respectively) and distance to escape terrain (similarly calculated) for each group location. Escape terrain was defined as "steep rocky terrain on which mountain sheep would safely outdistance or outmaneuver predators" (Gionfriddo and Krausman 1986). Escape terrain was characterized by rugged terrain or cliffs with slope >60%, and was present in a nearly contiguous 16-km x ≥0.5-km band on the west side of PJR. We surveyed and mapped escape terrain and water sources during August 1990.

We recorded habitat type and, when possible, number of individuals for each ram group observation. Habitat type definitions were based on vegetative and physiographic features thought to be important to bighorn sheep, including dominant grass and shrub species, presence and density of trees, and steepness (Buechner 1960, Geist 1971, Shannon et al. 1975, Risenhoover and Bailey 1985, Wakelyn 1987).

Mean herbaceous and shrub species canopy cover, shrub height, and shrub density were estimated for each habitat type by methods similar to those of Poulton and Tisdale (1961). We established 3 50-m line transects in representative stands of vegetation within each habitat type during June 1991, at peak forb abundance. Percent herbaceous cover was visually estimated within 20-cm x 50-cm plots placed every 5 m along each transect (Daubenmire 1959). The number of shrubs rooted in a 1-m belt adjacent to each transect was counted to estimate shrub density. Mean shrub height was calculated by measuring the individual shrub nearest each 5-m point on each transect. Percent canopy cover of shrubs was determined by the line intercept method (Canfield 1941).

In habitats with trees, we estimated tree density by the nearest neighbor method (Cottam and Curtis 1956). We randomly selected 50 trees/habitat and measured distance to the nearest tree. We calculated density as $2d^{-2}$, where d was the mean distance between nearest neighbors.

We used the minimum convex polygon method (Southwood 1966) with group locations as individual fixes to characterize herd ranges during spring (7 April-10 June) and summer (11 June-31 August). Chi-square contingency table analyses were used to compare frequency distributions of habitat type use, distance to escape terrain, distance to water, slope and elevation between seasons. We excluded aspect because it varied little over the area occupied by rams. If $\underline{P} < 0.05$, we constructed 95% simultaneous confidence intervals using the Bonferroni approach (Neu et al. 1974) to determine which habitats or physiographic attributes were used differently between seasons. Because these analyses were limited to comparisons between seasons (i.e., this was not a use/availability study), the areal extent of each habitat feature was not considered.

We used logistic regression (Meyers 1990:317-332) to model seasonal change in use of physiographic characteristics. Potential explanatory variables were distance to escape terrain, distance to water, slope and elevation. Season (spring or summer) was the response variable. We constructed a full model with main effects, quadratic terms, and 2-way interactions, then eliminated variables in a step-wise fashion if $\underline{P} > 0.05$ (Baker and Nelder 1985). Performance of reduced models was assessed by examination of the -2 log likelihood statistic for the contribution of explanatory variables (SAS Institute, Inc. 1990:1088-1089). We also determined the sensitivity (percent of observed event responses with predicted probability of event > 0.50), specificity (similar statistic for no event responses) and overall correct classification rate of the models (SAS Institute, Inc. 1990:1091-1092). If the final model included only 2 main effects, we generated a response surface by plotting the main effects against predicted probability of response to aid in model interpretation (Murtaugh 1988).

Mean ram group sizes by month were compared using a one-way analysis of variance. Post hoc pairwise comparisons were made with Scheffe's procedure (Milliken and Johnson 1992:35-36).

Results

Habitat Use

We identified 6 habitat types: Low sagebrush (*Artemisia arbuscula*) plateau (LSP), low sagebrush-bunchgrass (LSB), cliff-shrub (CS), juniper-low sagebrush (JLS), juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*) (JMBS), and Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass (WBSB) (Table 1). The LSP habitat type occupied the PJR plateau above 1,830 m. The LSB habitat type occurred on the PJR plateau below 1,830 m, and on the gentle east-facing slopes above Catlow Valley. The CS habitat type was found on the precipitous west face of PJR, and included the escape cover available to rams on this range. Much of the CS habitat type was bare rock, but vegetation occurred on narrow horizontal benches and in some gullies. The JLS and JMBS habitat types were found at mid- to low elevations on the east side of PJR, and were characterized by an overstory of western juniper with a sagebrush-bunchgrass understory. They differed primarily in tree density (9.7 vs. 90.8 trees/ha in the JLS and the JMBS, respectively) and the nature of the understory. The JMBS habitat type occurred in association with small canyons and rocky breaks. The WBSB habitat type occupied the floor of Catlow Valley near Rock Creek.

We observed 60 and 94 ram groups during spring and summer, respectively. In spring, rams generally occupied the upper PJR plateau <2 km from the rim. In mid-summer they expanded their range to include the east slopes and Catlow Valley near Rock Creek, which was a water source. When the creek went dry in mid-August, ram distribution shifted to the south end of PJR in the vicinity of Petroglyph Lake, which was a late summer water source. Observed spring and summer herd ranges were 24.4 and 74.5 km^2, respectively.

Ram habitat use differed between spring and summer ($\underline{X}^2 = 34.4$, 5 df, $\underline{P} < 0.001$) (Figure 1). The LSP habitat was used more frequently in spring, and the JLS and WBSB habitats were used

TABLE 1. Characteristics of shrubby and herbaceous vegetation in bighorn ram (*Ovis canadensis californiana*) habitats on Poker Jim Ridge, Oregon, June 1991.

	Shrubs			Grasses	Forbs
Habitat	Total Canopy Cover (%)	Density (no./m2)	Mean Height (cm)	Total Canopy Cover (%)	Total Canopy Cover (%)
Low sagebrush (*Artemisia arbuscula*) plateau	17.8	1.9	16.8	8.1	16.8
Low sagebrush-bunchgrass	20.7	1.4	23.3	15.0	18.3
Cliff-shrub[a]	32.1	1.8	27.2	6.2	8.4
Juniper (*Juniperus occidentalis*)-low sagebrush	17.6	1.4	23.4	25.5	15.6
Juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*)	25.9	0.7	82.0	7.3	12.1
Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass	14.9	0.8	50.1	11.9	4.6

[a]Results reflect characteristics within islands of vegetation.

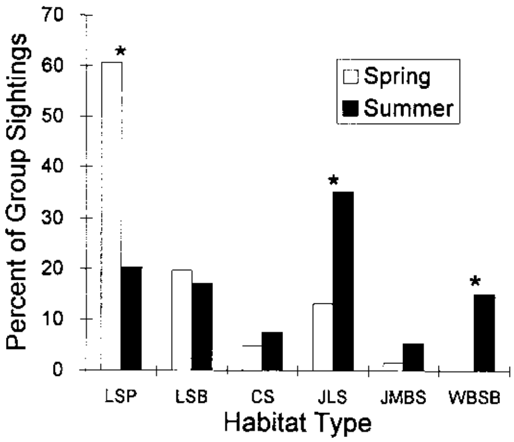

Figure 1. Percent use of habitat types by bighorn ram (*Ovis canadensis californiana*) groups on Poker Jim Ridge, Oregon, spring and summer 1990. LSP = low sagebrush (*Artemisia arbuscula*) plateau, LSB = low sagebrush-bunchgrass, CS = cliff-shrub, JLS = juniper (*Juniperus occidentalis*)-low sagebrush, JMBS = juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*), WBSB = Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass. * = Significant difference in use between spring and summer based on 95% simultaneous confidence intervals.

more frequently in summer. The CS and JMBS habitats received little use in either season.

Significant differences were found in use of physiographic characteristics between spring and summer (Figure 2). Ram groups were found closer to escape terrain in spring ($\underline{X}^2 = 17.6$, 3 df, $\underline{P} < 0.001$). Sixty-five percent of spring locations but only 40% of summer locations were within 1 km of escape terrain. We commonly observed rams >3 km from escape terrain in summer (25.5% of summer locations). In spring, rams tended to be farther from water ($\underline{X}^2 = 26.5$, 3 df, $\underline{P} < 0.001$), on gentler slopes ($\underline{X}^2 = 9.16$, 2 df, $\underline{P} = 0.01$), and at higher elevations ($\underline{X}^2 = 19.32$, 2 df, $\underline{P} < 0.001$).

The most parsimonious logistic regression model for differentiating use of physiographic characteristics between spring and summer included main effects and quadratic terms for distance to escape terrain and water, and a significant distance-to-escape terrain x distance-to-water interaction (Table 2). The contribution of the variables to the fitting of the model was significant ($\underline{X}^2 = 50.66$, 5 df, $\underline{P} < 0.001$). The addition of elevation to this model significantly decreased model deviance ($\underline{X}^2$ approximation = 6.48, 1 df,

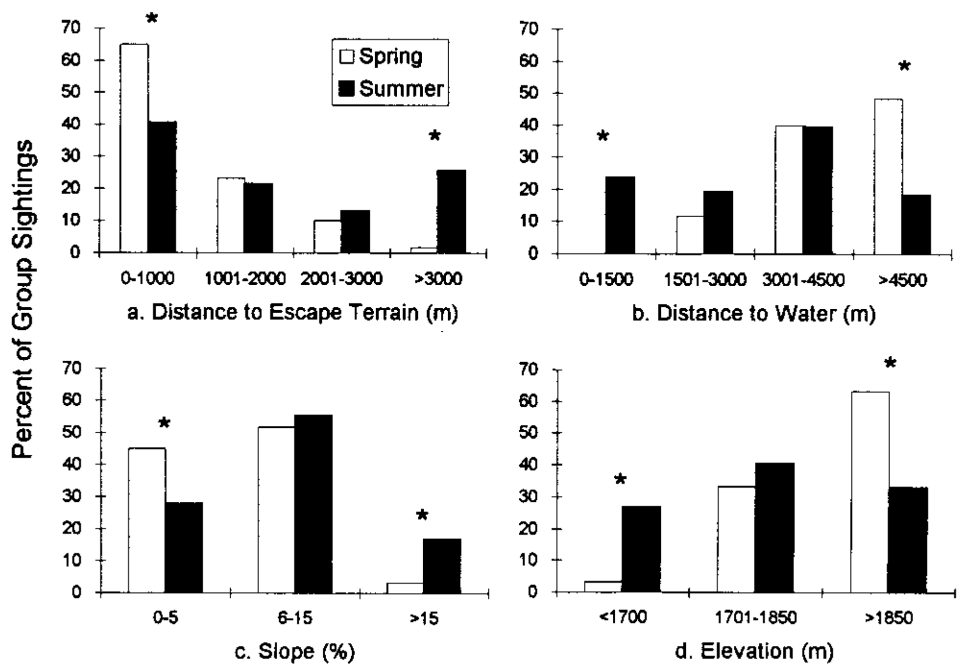

Figure 2. Comparison of bighorn ram (*Ovis canadensis californiana*) group distribution on Poker Jim Ridge, Oregon between spring and summer 1990 in relation to (a) distance to escape terrain, (b) distance to water, (c) slope, and (d) elevation. * = Significant difference in use between spring and summer based on 95% simultaneous confidence intervals.

TABLE 2. Estimated coefficients from logistic regression of probability of a bighorn ram (*Ovis canadensis californiana*) group observation on Poker Jim Ridge, Oregon in spring and summer 1990 occurring in spring against distances to escape terrain (m) and water (m).

Variable	Estimated Coefficient	Standard Error
Intercept	-14.33	5.129
Distance from escape terrain	9.151×10^{-3}	3.100×10^{-3}
(Distance from escape terrain)^2	-1.475×10^{-6}	5.145×10^{-7}
Distance from water	4.378×10^{-3}	1.774×10^{-3}
(Distance from water)^2	-2.741×10^{-7}	1.623×10^{-7}
(Distance from escape terrain) x (Distance from water)	-1.521×10^{-6}	4.997×10^{-7}

P = 0.011), but elevation was highly correlated with distances to escape terrain and water (Pearson's r = -0.820 and 0.829, respectively). The standard errors of the coefficients of the other variables decreased substantially when elevation was dropped, further emphasizing the collinearity. Sensitivity, specificity and overall correct classification rate of the model were 72.1%, 71.4% and 71.7%, respectively. A response surface generated by plotting distances to escape terrain and water against the predicted probability of a ram group observation occurring in spring demonstrated that ram groups were predicted to most likely occur <2 km from escape terrain and >6 km from water sources during spring (Figure 3). Areas farther from escape terrain and closer to water were predicted to be used more during summer.

Group Size

We observed 1,139 rams in 146 groups. Ram group size varied by month (F = 13.87, 4, 141 df,

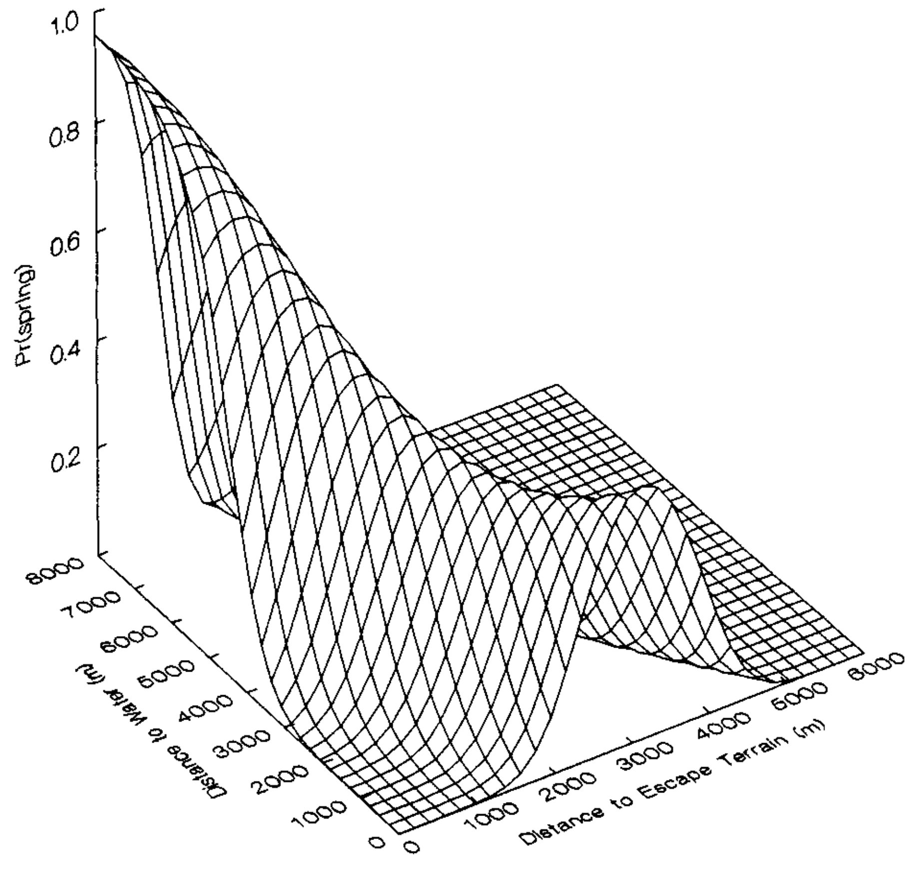

Figure 3. Response surface generated from logistic regression model for differences in distance to escape terrain and water for bighorn ram (*Ovis canadensis californiana*) groups on Poker Jim Ridge, Oregon between spring and summer 1990. Pr(spring) = predicted probability of a group observation at a site described by the response surface occurring in spring.

TABLE 3. Mean size of bighorn ram (*Ovis canadensis californiana*) groups by month, April through August 1990, Poker Jim Ridge, Oregon.

Month	N ram groups encountered	Mean group size (± s.d.)[a]
April	26	12.19 (± 7.32)*
May	24	10.67 (± 6.26)*
June	29	10.03 (± 7.66)*
July	43	4.21 (± 2.91)**
August	24	3.92 (± 3.20)**

[a]Asterisks indicate results of Scheffe's test for pairwise comparisons. Means with different numbers of asterisks are significantly different ($P < 0.05$).

$P < 0.001$) (Table 3). There were no significant pairwise differences between mean group sizes in April, May and June ($P > 0.70$ for all comparisons), or July and August ($P > 0.90$). Ram groups were smaller during July-August than April-June ($P < 0.01$ for all pairwise comparisons).

Discussion

Bighorn ram herd range size increased three-fold between spring and summer. We observed no distinct migration, but rather a gradual expansion into contiguous areas. Herd range size is a function of individual home ranges within a herd and the degree of overlap between those ranges. Bighorn sheep are gregarious (Blood 1963, Simmons 1980), and home ranges within a herd can overlap considerably (Leslie and Douglas 1979). Thus, increased herd range size probably reflected increases in home range size, rather than dispersal of individuals or small groups.

Habitat quality, determined by the availability and juxtaposition of forage, water and escape terrain, is an important determinant of seasonal home range size in bighorn sheep (Krausman et al. 1989). On PJR, escape terrain was obviously constant, but forage and water availability generally decreased from spring to summer. Herd range size increased during the period, consistent with the hypothesis that resource limitations cause bighorn sheep to range over larger areas to satisfy physiological needs (Leslie and Douglas 1979).

The logistic regression model we developed for differentiating use of physiographic characteristics identified variables that explained the majority of variation between seasons. No causality was inferred from the model itself, but knowledge of physiological and behavioral requirements of bighorn rams and the availability of resources on PJR allowed speculation regarding reasons for observed differences. The model was limited by the explanatory variables chosen for inclusion, and obviously other biotic and abiotic factors (e.g., visibility, forage composition and quality) could have affected ram distribution. However, slope, elevation, aspect, and proximity to escape terrain and water are known to be important determinants of habitat use (Shannon et al. 1975, Tilton and Willard 1982, Risenhoover and Bailey 1985, Gionfriddo and Krausman 1986, Krausman and Leopold 1986, Fairbanks et al. 1987, Wakelyn 1987), and bighorn sheep are opportunistic foragers, adapting their diet to available plant communities (Keating et al. 1985, Miller and Gaud 1989). Thus, we chose not to include vegetative association as a potential explanatory variable in the model. We defined habitat types based on physiographic and vegetative features, however, so differences in use of habitat types between seasons provided additional insight into differential use of habitat.

Observed movements of PJR rams between spring and summer probably resulted from changing water requirements associated with changes in forage succulence and availability of ephemeral water sources. In mid-summer, ram activity shifted from the upper plateau to the east slopes and Catlow Valley near Rock Creek. In late summer, Rock Creek dried up and use shifted toward Petroglyph Lake. The lake was much less remote, being within sight of the refuge access road and receiving some human use, but was closer to escape terrain. The former may have contributed to its being a "second choice" water source, while the latter may have helped to offset effects of human disturbance.

Distances to water and escape terrain were significant explanatory variables in the final model differentiating spring and summer habitat use (Table 2). The response surface generated by this model over the range of observed values for explanatory variables demonstrated that the model predicted movement of rams away from the upper plateau (close to escape terrain, far from water) toward Rock Creek (far from escape terrain, close to water) and Petroglyph Lake (close to escape terrain and water) in summer (Figure 3) (note that pr[spring] on the z-axis is equivalent to 1-pr[summer]).

Differences in use of habitat types between spring and summer (Figure 1) also reflected the trend of dispersal from the upper plateau (predominantly LSP) in early summer and utilization of Rock Creek, which was within the WBSB habitat type. Use of JLS also increased during summer. This habitat type provided thermal cover, had the greatest grass canopy cover of any PJR habitat (Table 1), and may have held succulent forage longer due to favorable microclimates created by shade of juniper trees. Mean tree density was relatively low (9.7 trees/ha), so visibility was probably not substantially compromised. Use of the JMBS habitat type did not differ between seasons, even though it was interspersed with JLS habitat type. Mean tree density here was much greater (90.8 trees/ha) and grass canopy less (Table 1), making it a less suitable bighorn sheep habitat (Shannon et al. 1975, Tilton and Willard 1982, Wakelyn 1987).

Ram group size during April-June was more than twice that during July-August (Table 3). Festa-Bianchet (1986) hypothesized that large spring concentrations of Rocky Mountain bighorn rams (*Ovis canadensis canadensis*) in Alberta provided opportunities to develop social skills important for future reproductive success. Other studies have suggested that group size is an indicator of habitat quality, with high quality forage conditions favoring larger groups (Berger 1979, Leslie and Douglas 1979, Simmons 1980). We observed smaller groups during summer when resources were probably more limited, consistent with the latter theory.

It has also been suggested that larger groups enhance predator surveillance, allowing sheep to spend more time foraging and to use habitats farther from escape terrain or with decreased visibility (Risenhoover and Bailey 1985, Warrick and Krausman 1987, Krausman et al. 1989), although there may be little added benefit beyond 5 individuals (Berger 1978). On PJR group size declined coincident with use of less secure habitats, i.e. those further from escape terrain with greater shrub height (WBSB) and presence of trees (JLS). In no month was the upper bound of the 95% confidence interval for mean group size <5, however (Table 3). During this study there were no known predators of adult bighorn sheep on PJR other than humans during 2 1-week hunting seasons in September (W. Pyle, U. S. Fish Wildl. Serv., pers. comm.), and most of the ram range was remote and received little human use. These factors probably released rams from the constraints often associated with use of less secure habitats, allowing them to adapt group size to available resources.

Our data suggested that water availability exerted a major influence on the seasonal distribution of bighorn rams in this population. Rams traveled >5 km from escape terrain and used habitats with reduced visibility to obtain water. We attributed this to a lack of predators and minimal human disturbance. Although bighorn rams may tolerate moderate predation risk to obtain access to high quality habitat, disturbance and habitat degradation due to recreation or cattle grazing could have deleterious effects on a seasonally shifting population (Bleich et al. 1997). Further, seasonal shifts in distribution are unlikely to be rigidly repeated, but rather respond dynamically to changing environmental conditions (Leslie and Douglas 1979, Festa-Bianchet 1986). If this study had been conducted in a year when Rock Creek remained a reliable water source through late summer, for instance, the importance of Petroglyph Lake may not have been realized. Thus it is important to identify habitat requirements under a variety of environmental conditions, and provide adequate protection to sustain seasonal shifts in distribution.

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