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Bitterbrush and cheatgrass quality on 3 southwest Idaho winter ranges

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Abstract

Nutritional stress is an important mortality factor for wintering mule deer (*Odocoileus hemionus hemionus* Rafinesque), particularly fawns. The rate at which fawns utilize existing fat stores is at least partially dependent upon the quality of available forage during winter. Although numerous studies have determined the nutritive value of various forage species, more research is needed to determine whether individual forage species vary in quality across the landscape. We determined whether differences existed in the nutritional quality of antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) and cheatgrass brome (*Bromus tectorum* L.) among 3 winter ranges and 6 habitats within the winter ranges. In vitro dry matter digestibility (IVDMD) of bitterbrush varied among winter ranges in 1996 and 1997 ($P < 0.001$). The highest mean IVDMD measured on a winter range was 29.8% ($n = 36$, SD = 3.87) in 1997 while the lowest was 15.2% ($n = 38$, SD = 4.42) in 1996. Bitterbrush crude protein (CP) was different among habitats in 1997 ($P = 0.005$), with mean CP values ranging from 7.0% ($n = 19$, SD = 0.73) to 8.0% ($n = 13$, SD = 0.70). The length and diameter of available bitterbrush leaders varied within and among winter ranges because of differential utilization. Bitterbrush IVDMD and CP varied in relation to the mean diameter of leaders obtained from each random sampling site ($P < 0.001$). The quality of bitterbrush decreased as browse intensity increased. Cheatgrass IVDMD was different between winter ranges ($P < 0.001$) in 1996, with mean values ranging from 65.8% ($n = 36$, SD = 4.34) to 69.6% ($n = 36$, SD = 3.83). Site-specific variation should be considered when evaluating the nutritional quality of mule deer habitat, at least during winter when species diversity in deer diets is limited.

Key Words: nutritional quality, mule deer, in vitro dry matter digestibility, crude protein, *Purshia tridentata*, *Bromus tectorum*

Resumen

El estrés nutricional es un factor importante de mortalidad invernal en los venados (*Odocoileus hemionus hemionus* Rafinesque), particularmente para los cervatos. La tasa a la cual los cervatos utilizan las reservas existentes de grasa es parcialmente dependiente de la calidad de forraje disponible durante el invierno. Aunque numerosos estudios han determinado el valor nutritivo de varias especies forrajeras se necesita más información para determinar si las especies forrajeras individuales varían en calidad a través del terreno. Determinamos si existen diferencias en la calidad nutricional del "Antelope bitterbrush" (*Purshia tridentata* [Pursh] DC.) y "Cheatgrass brome" (*Bromus tectorum* L.) entre 3 pastizales de invierno y 6 hábitats dentro de los pastizales de invierno. En 1996 y 1997, la digestibilidad in vitro de la materia seca (DIVMS) del "Bitterbrush" varió entre los pastizales de invierno ($P < 0.001$). El mayor promedio de DIVMS obtenido en un pastizal de invierno fue de 29.8% (n = 36, SD = 3.87) en 1997, mientras que el menor promedio fue 15.2% (n=38, SD = 4.42) en 1996. En 1997, la proteína cruda (PC) de "Bitterbrush" fue diferente entre hábitats ($P = 0.005$), con valores promedio de PC en un rango de 7.0% (n = 19, SD = 0.73) a 8.0% (n = 13, SD = 0.70). La longitud y diámetro de los tallos principales de "Bitterbrush" disponible variaron entre los pastizales de invierno debido a diferenciales de utilización. La DIVMS y PC del "Bitterbrush" variaron en relación al diámetro promedio de los tallos pincipales obtenidos de cada sitio aleatorio de muestreo ($P < 0.001$). La calidad del "Bitterbrsuh" disminuyó conforme la intensidad del ramoneo aumento. En 1996, la DIVMS del "Cheatgrass" fue diferente entre los pastizales de invierno ($P < 0.001$), con valores promedio en un rango de 65.8% (n = 36, SD = 4.34) a 69.6% (n = 36, SD = 3.83). La variación especifica por sitio debe ser considerada al evaluar la calidad nutricional del hábitat del venado, al menos durante el invierno cuando la diversidad de especies en la dieta del venado es limitada.

Winter malnutrition is a common cause of mortality for mule deer (*Odocoileus hemionus hemionus* Rafinesque) fawns, particularly during severe winters. Nutritionally stressed fawns are also more susceptible to other proximal causes of mortality. Since mule deer largely depend on pre-winter fat stores to meet energy requirements during winter, over-winter fawn survival is often determined by the duration and severity of winter (Wallmo et al. 1977, Torbit et al. 1985). Nutritional stress arises from a lack of necessary quality in forage to sustain mule deer through winter (Wallmo et al. 1977). Although nutritional maintenance requirements are rarely met, differences in the nutritive value of the forage may be very important. Deer selecting higher quality diets should deplete existing fat stores more slowly, thereby increasing the probability of survival.

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Digestibility, protein, and other indices of nutritional quality have been determined for numerous plant species eaten by mule deer (Bissell and Strong 1955, Trout and Thiessen 1973, Welch 1989, Austin et al. 1994). However, assigning a single nutritional value such as digestibility or protein to a particular forage species may not be appropriate. Relatively little research has focused on differences in quality within the same plant species. Intraspecies variation occurs as a result of genetic variability (Welch and McArthur 1979, Welch and Pederson 1981, Welch et al. 1983a, Welch 1989) and environmental factors (Laycock and Price 1970). Aside from documenting seasonal differences in quality, intraspecies variation resulting from environmental factors has been studied very little. Environmental variables which may differentially affect forage quality include temperature, precipitation/leaching, light intensity, various soil attributes, habitat type, aspect, slope, elevation, and grazing (Laycock and Price 1970). Intraspecies relationships may be particularly important in rangelands during winter, where mule deer diets comprise fewer species because the diversity of available forage is low compared to other seasons or other ecosystems.

Our goal was to evaluate intraspecies variation in nutritional quality during a short time interval (3–4 weeks) while limiting spatial variation to a portion of southwest Idaho (4950 km^2). We sampled bitterbrush (*Purshia tridentata* [Pursh] DC.) and immature, green cheatgrass (*Bromus tectorum* L.), which are both used by mule deer on southwest Idaho winter ranges. Trout and Thiessen (1973) and Scholten (1983) found that bitterbrush comprised roughly one-third of the diet of mule deer during peak winter use in southwest Idaho, indicating a strong preference when availability was considered. Scholten (Idaho Department of Fish and Game, unpublished) found that bitterbrush, on average, comprised only 15% of the available annual growth (kg ha^{-1}) of sagebrush (*Artemisia* spp. L.), bitterbrush, and rabbitbrush (*Chrysothamnus* spp. Nutt.). Austin et al. (1994) found cheatgrass to be one of several annual grasses which are nutritionally valuable to mule deer when green during the spring and fall. We determined whether differences existed in the nutritional quality of bitterbrush or cheatgrass among 3 mule deer winter ranges and among 6 habitat components in southwest Idaho, and to what extent bitterbrush quality may differ from one year to the next. We assessed nutritional quality by determining in vitro dry matter digestibility (IVDMD) and crude protein (CP).

Materials and Methods

Study Areas

Our research was conducted on 3 winter ranges in southwest Idaho. Mule deer were present on each winter range from December to early May. The Bennett Hills winter range (43°08'N 115°15'W), located 12 km north of Glenns Ferry, Ida., included the King Hill Creek and Little Canyon Creek drainages and adjacent plateaus. The area included 270 km^2 with elevations ranging from 773 m at lower King Hill Creek to 1,585 m on the upper plateaus adjacent to Little Canyon Creek. The Blacks Creek winter range (43°30'N 116°00'W) was located 15 km east of Boise, Ida., along the lower portion of the Boise River drainage. The area included 120 km^2 with elevations ranging from 950 m near Boise to 1,525 m near Three Point Mountain. The Owyhee winter range (43°10'N 116°50'W), located 45 km southwest of Boise, included the Reynolds Creek drainage. The area was 375 km^2 with elevations ranging from 750 m at lower Reynolds Creek to 1,700 m on Whiskey Mountain (Bishop 1998). Climate data for each winter range is located in Table 1.

Seven habitat components were broadly defined with 2 considerations. First, we tried to identify habitats that could be found in all 3 winter ranges. Second, we were interested in vegetation structure and cover as well as species composition. Classifications of habitat component were high shrub (> 50% shrub cover, majority of shrubs > 1 m tall), scattered high shrub (20–50% shrub cover, majority of shrubs > 1 m tall), low shrub (> 50% shrub cover, majority of shrubs <1 m tall), scattered low shrub (20–50% shrub cover, majority of shrubs <1 m tall), grass (<20% shrub cover), rock (> 70% rock cover), and riparian. In addition to bitterbrush, high shrub habitats were dominated by basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) and Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* Beetle and Young). Low shrub habitats primarily consisted of Wyoming big sagebrush and low sagebrush (*A. arbuscula* Nutt.). Mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle) occasionally occurred in both high and low shrub habitats. Rock habitat was virtually absent from Blacks Creek. In addition to cheatgrass, grass species common among the winter ranges included wheatgrasses (*Agropyron* spp.), bluegrasses (*Poa* spp.), Idaho fescue (*Festuca idahoensis* Elmer), medusahead (*Taeniatherum caput-medusae* L.), squirrel tail (*Sitanion hystrix* [Nutt.] Smith), and Great Basin wildrye (*Elymus cinereus* Scribn. and Merr.).

Fire, Grazing, and Soils

Seventy-five percent of the Blacks Creek winter range burned in 1992. As a result, much of the area consisted of annual grassland habitats. Unburned portions of the area were used heavily by mule deer when snow prevented access to grasses, and vegetative cover was presumably necessary. No recent burns had occurred on either the Bennett or Owyhee winter ranges. All 3 winter ranges were grazed by cattle. The most intensive cattle grazing occurred on unburned private land in Blacks Creek from December through May ($\bar{x}$ = ~1.3 AUM's/ha). This private land comprised a relatively small portion of the overall winter range, but received much deer use. The remainder of the Blacks Creek range received minimal grazing. Management of grazing on the Bennett and Owyhee winter ranges was through Bureau of Land Management (BLM). The various allotments were grazed at different times and variable intensities from spring through fall, averaging approximately 0.2 AUM's/ha overall.

Table 1. Mean temperature and total precipitation obtained from weather stations in 3 mule deer winter ranges in southwest Idaho, 1995–97 (WRCC 1998).

		Mean Temperature			Total Precipitation		
Year	Season	Bennett	Blacks Cr	Owyhee	Bennett	Blacks Cr	Owyhee
		(°C)			(cm)		
1995–96	Jun.–Aug.	20.6	20.2	18.2	3.4	5.7	5.2
	Sep.–Nov.	11.6	11.2	9.9	5.7	9.3	6.1
	Dec.–-Feb.	0.5	0.5	-0.2	11.7	20.1	13.3
	Mar.–May	10.0	9.5	7.9	10.5	14.8	11.0
1996–97	Jun.–Aug.	22.2	22.1	19.5	1.1	1.1	3.3
	Sep.–Nov.	10.5	10.5	9.0	7.6	9.7	6.8
	Dec.–Feb.	1.0	0.8	1.4	16.2	27.7	18.8
	Mar.–May	10.7	10.7	9.0	4.2	9.8	8.0

The Bennett winter range was located on a mafic volcanic flow, with soils having a basaltic origin. The Blacks Creek winter range primarily contained granitic soils from a calcium-alkaline intrusive formation. The Owyhee range covered both intrusive and extrusive rock formations, with soils derived from granite, ryolite, and basalt (Johnson and Raines 1995). Soil types comprising each winter range were primarily Aridisols and Mollisols. In both the Blacks Creek and Owyhee winter ranges, 75% of the bitterbrush and cheatgrass samples were collected from Mollisols while the remaining 25% were from Aridisols (NRCS 1999a,1999c). In the Bennett winter range, 28% of samples were collected from Mollisol soils, 27% from Aridisols, 23% from rocky substrate, 16% from Vertisols, and 5% from Inceptisols (NRCS 1999b). In terms of texture, 90% of the Blacks Creek samples were from loamy soils while the remainder were from gravelly soils. In the Bennett range, 34% of sample sites comprised shallow stony loam soils, 23% comprised loamy soils, 20% sandy loam, and 23% were from rocky substrate. In the Owyhee range, 42% of sampling sites were loamy soils, 42% were shallow claypans, and 16% were sandy loams (NRCS 1999a,1999b, 1999c).

Experimental Design and Random Sampling Procedure

We collected 108 cheatgrass samples between 28 March and 26 April 1996. We collected 109 bitterbrush samples during both 1996 (20 February–13 March) and 1997 (22 February–17 March) from permanent plots. Cheatgrass sampling was not repeated in 1997 because nutritional values in 1996 were high and only minor differences due to location were observed. Intraspecific variation in cheatgrass quality would have to be large to impact mule deer survival and fitness given its high nutritional quality. Bitterbrush and cheatgrass samples were collected from 6–7 randomly selected patches of each of 6 habitat components within each winter range. Of the 7 habitat components previously defined, we did not sample bitterbrush from riparian habitat because of low prevalence, and we did not sample cheatgrass from rock habitat due to insufficient quantity. The experimental design for cheatgrass was a completely randomized design in a 3 x 6 arrangement of treatments. The experimental design for bitterbrush was a repeated measures through time in a completely randomized design with a 3 x 6 arrangement of treatments and a missing plot. The missing plot occurred because rock habitat was absent in the Blacks Creek range.

Random sampling sites were generated within each study area as latitudes and longitudes from a random numbers table and located in the field using a Garmin Global Positioning System. We collected bitterbrush and cheatgrass samples from a different winter range and multiple habitats each day so that treatments would not be confounded with any temporal variation. Within each randomly selected habitat patch, one forage sample ($\geq$ 10 g dry weight) was collected from a 20 m radius-circular plot. We sampled most cheatgrass within the circular plot or ~10 bitterbrush plants. Each habitat patch sampled was isolated from all other patches of the same habitat component.

We recorded slope and aspect in degrees at each sampling site. Aspect values were converted to a 180° scale where northeast (45°) represented 0° and southwest (225°) represented 180°. We used ARC/INFO and ArcView software (E.S.R.I. 1996, 1997) to obtain soil and precipitation data corresponding to each site. Soil particle size and soil depth (cm) were determined from digital soil surveys (NRCS 1999a, 1999b, 1999c), and total yearly precipitation (mm) during a normal year was obtained from a digital precipitation model (Thornton et al. 1997). Soil particle size was evaluated on a continuous gradient from very fine to course particles. When sampling bitterbrush during 1996, it was visually apparent that leader length and diameter varied between sites as a result of utilization from both deer and cattle. In 1997, we recorded the mean diameter (mm) of the available leaders at each site to assess the influence of browse intensity on bitterbrush quality.

Determination of IVDMD and CP

Bitterbrush leaders and green cheatgrass were harvested by hand in a manner which simulated observed foraging behavior of mule deer (Sowell et al. 1985). Samples were air dried at a room temperature of 21°C. Dried bitterbrush samples were initially ground with a Wiley Mill using a 2 mm screen. Samples were then ground a second time using a Cyclone Mill with a 1 mm screen in place. Cheatgrass samples were ground using a coffee grinder so that minimal sample was lost during the grinding process. Ground cheatgrass comprised exceptionally fine, homogeneous particles which eliminated the need for a filter screen. Dry matter was determined by oven drying samples at 100°C (A.O.A.C. 1990). To determine IVDMD, we used the first stage of the Tilley and Terry (1963) technique as modified by Pearson (1970). The rumen inoculum source for the estimation of digestibility was obtained from Hereford-crossbred cows maintained on an alfalfa/barley diet. Welch et al. (1983b) found that different sources of rumen inocula, from both domestic and wild ruminants on different diets, similarly digested a wide variety of forages. Also, forage samples tend to be ranked correctly in terms of relative quality when different inocula sources are used (Robbins et al. 1975). Nitrogen content was analyzed by combustion using a Leco CHN 600 Analyzer. CP was determined by multiplying percent N by 6.25 (A.O.A.C. 1990).

Statistical Methods

The IVDMD and CP values were analyzed using a multivariate analysis of covariance (MANCOVA) type linear model with canonical analysis using PROC GLM in SAS (SAS Institute 1989). Winter range and habitat were the independent categorical variables, and year represented a repeated measure in the bitterbrush analysis. Covariates included Julian sampling date, slope, aspect, soil particle size, soil depth, and precipitation. Julian sampling date was selected as a covariate to determine whether nutritional quality varied temporally through the sampling period. Due to the missing cell in the experimental design for bitterbrush, Type IV sums of squares and cross products (*SS&CP*) were used. A variety of Type IV estimable functions existed for main effects and some interactions. In cases where the functions used by PROC GLM (SAS Institute 1989) excluded data, we developed meaningful functions that utilized all of the data. We then used PROC IML in SAS (SAS Institute 1995) to calculate the appropriate Type IV *SS&CP*, or hypothesis matrices. An extreme outlier in the bitterbrush data set, although biologically feasible, was removed to avoid violating the assumptions of multivariate normality and variance-covariance homogeneity.

We initially tested for differences in bitterbrush quality between winter ranges, habitats, years, and their interactions. Due to a significant winter range $\times$ year interaction, we ran separate analyses on bitterbrush quality for each year individually. For the 1997 bitterbrush data, mean leader diameter from each sampling site was included in the analysis as a covariate. For these analyses, as well as the analysis of cheatgrass quality, we tested for differences between winter ranges and habitats and the interaction. We were unable to test for differences between habitats within each winter range due to insufficient sample size and therefore low power. We used Wilks' lambda as the test statistic for all analyses, which was converted to an F statistic to evaluate significance. Each of the commonly used multivariate test statistics gave similar results. For each significant result, we proceeded with a canonical analysis. A canonical variable is a combination of dependent variables which explain variation among data points. The first canonical variable accounts for the greatest amount of variation in the data set, followed by the second canonical variable and so forth. Canonical variates were assessed by looking at both the standardized canonical coefficients and the within canonical structure (SAS Institute 1989). Analyses of covariance (ANCOVA) were performed on IVDMD and CP individually for any significant tests obtained from the MANCOVA. Tukey's studentized range test (HSD) was used to make pairwise mean comparisons of significant main effects obtained from the ANCOVA's.

Results

Bitterbrush Quality

Bitterbrush quality, evaluated in terms of IVDMD and CP, varied between winter ranges ($P < 0.001$) and years ($P < 0.001$) and there was a range × year interaction ($P < 0.001$). The first canonical variate for the interaction explained 99.9% of the variation in the eigenvalue structure, and was therefore the only canonical variable of interest. In vitro dry matter digestibility was the most important variable in describing canonical 1. Bitterbrush digestibility substantially increased from 1996 to 1997 in the Bennett and Owyhee winter ranges but slightly decreased in Blacks Creek. The main effect of habitat was not significant, nor were the range × habitat, habitat × year, and range × habitat × year interactions ($P > 0.10$).

In 1996, bitterbrush quality varied between winter ranges ($P < 0.001$) but not habitats ($P = 0.057$), and the range x habitat interaction was not significant ($P = 0.878$). Precipitation ($P = 0.051$) and soil depth ($P = 0.061$) effectively explained variation in the data and improved tests of the main effects. Sampling date ($P = 0.938$), aspect ($P = 0.645$), slope ($P = 0.262$), and soil particle size ($P = 0.774$) were ineffective covariates and therefore removed from the analysis. Canonical 1

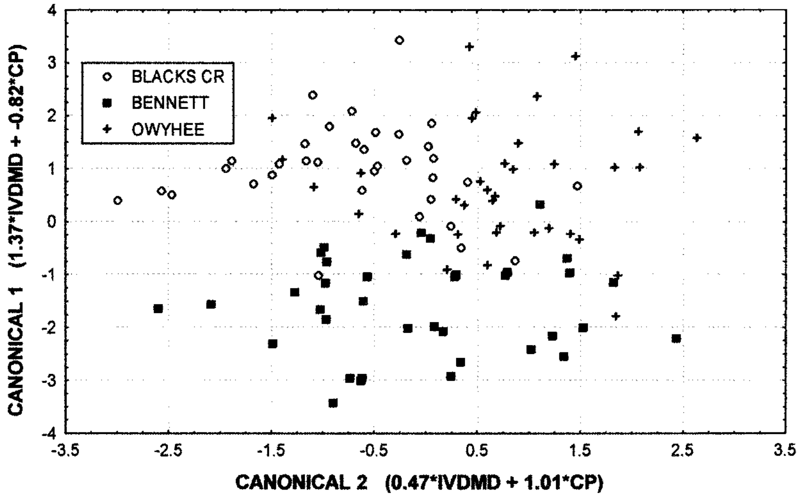

Fig. 1. Canonical plot of bitterbrush quality in relation to 3 mule deer winter ranges in southwest Idaho, 1996. Canonical 1 is the combination of in vitro dry matter digestibility (IVDMD) and crude protein (CP) that explains the most bitterbrush variation among winter ranges. The Blacks Creek and Owyhee ranges are distinguished from the Bennett range along this axis due mostly to IVDMD differences. Canonical 2 is the combination of IVDMD and CP that explains the next most variation among winter ranges. The Owyhee range is separated from Blacks Creek along this second axis due primarily to CP differences. The 2 canonical variables together distinguish each study area from the other.

for winter ranges explained 84% of the variation in the eigenvalue structure, while the second canonical accounted for the remaining 16% of the variation. Both canonical variates were significant ($P < 0.001$). In vitro dry matter digestibility was the most influential variable in canonical 1 (1.37*IVDMD + –0.82*CP), which distinguished the Bennett range from the Blacks Creek and Owyhee ranges. Crude protein explained the most variation in canonical 2 (0.47*IVDMD + 1.01*CP), which distinguished Blacks Creek from the Owyhee range (Fig. 1). For IVDMD, each of the 3 winter ranges were different from one another with $\alpha = 0.05$. Bitterbrush in the Owyhee winter range had the highest mean digestibility followed by Blacks Creek, while the Bennett range had the lowest mean digestibility. For CP, the Blacks Creek range was significantly lower than both the Bennett and Owyhee ranges, which were not significantly different (Table 2).

In 1997, mean leader diameter of bitterbrush from each sampling site was included in the analysis as a covariate. In 1997, bitterbrush quality varied between winter

Table 2. In vitro dry matter digestibility (IVDMD) and crude protein of bitterbrush for 3 mule deer winter ranges and 6 habitat components in southwest Idaho, 1996–97.

Treatment	Class	IVDMD				Crude Protein			
		1996		1997		1996		1997	
		$\bar{x}$[1]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
		(%)				(%)			
Winter Range	Bennett	15.2[a]	4.42	23.2[b]	4.74	7.3[b]	0.59	7.3	0.76
	Blacks Creek	21.9[b]	3.74	20.4[a]	4.76	6.5[a]	0.53	7.2	0.67
	Owyhee	24.6[c]	4.42	29.8[c]	3.87	7.2[b]	0.54	7.5	0.71
Habitat	High Shrub	21.7	5.41	24.6	5.11	7.1	0.60	7.1[a]	0.59
	Low Shrub	20.1	5.43	24.8	6.44	6.8	0.66	7.3[a]	0.74
	Scattered High Shrub	20.8	5.49	24.0	6.90	7.2	0.70	7.4[ab]	0.71
	Scattered Low Shrub	19.1	6.59	23.6	4.81	6.7	0.71	7.0[a]	0.73
	Grass	20.3	4.87	24.4	6.65	7.0	0.60	7.3[a]	0.67
	Rock	20.8	7.62	26.5	5.17	7.4	0.42	8.0[b]	0.70
Overall	Total Sample	20.5	5.78	24.5	5.85	7.0	0.66	7.3	0.72

[1]Within columns for each treatment, means with the same letter are not significantly different ($P > 0.05$). Letter superscripts are included only where post hoc mean comparisons were warranted.

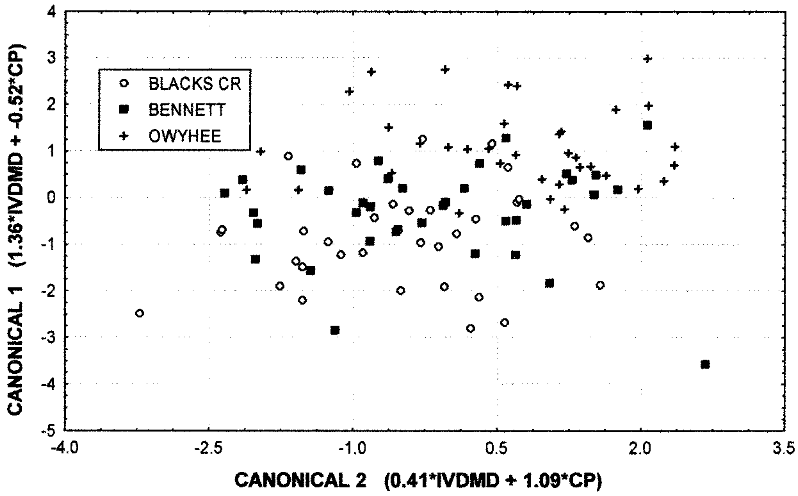

Fig. 2. Canonical plot of bitterbrush quality in relation to 3 mule deer winter ranges in southwest Idaho, 1997. Canonical 1 is the combination of in vitro dry matter digestibility (IVDMD) and crude protein (CP) that explains the most bitterbrush variation among winter ranges. The 3 ranges are reasonably separated along the canonical 1 axis as a result of IVDMD differences. The canonical 2 axis, driven by CP, does not provide any separation of the winter ranges, indicating that CP differences were minor.

ranges (P < 0.001) and habitats (P = 0.035), and the range × habitat interaction was not significant (P = 0.342). Bitterbrush leader diameter was significant (P < 0.001), indicating that utilization of leaders by deer and cattle influenced quality. Sampling date (P = 0.403), soil particle size (P = 0.370), soil depth (P = 0.370), precipitation (P = 0.841), aspect (P = 0.585), and slope (P = 0.286) did not explain variation in the data and were removed from the analysis. Canonical 1 for study areas accounted for 94% of the variation in the eigenvalue structure and was the only significant canonical. The IVDMD was the most important variable for explaining variation in canonical 1 (1.36*IVDMD + –0.52*CP), which distinguished each winter range from the others (Fig. 2). Canonical 1 for habitats (–0.10*IVDMD + 1.20*CP) explained 94% of the variation in the data, but CP was the most important variable. Thus, winter ranges varied as a result of differences in digestibility while habitats varied in response to protein differences. Each of the winter ranges were different from one another in terms of IVDMD. Bitterbrush from the Owyhee range had the greatest digestibility followed by the Bennett range, while that from Blacks Creek had the least digestibility. For habitat differences in CP, rock was greater than all other habitats except scattered high shrub, which was not significantly different from any other habitat (Table 2). For the leader diameter covariate, both IVDMD and CP were important in explaining the single canonical variable. As leader diameter of bitterbrush increased, both IVDMD and CP decreased (P < 0.001) (Fig. 3). Differences in leader diameter were a function of browse intensity, indicating that bitterbrush quality decreased as leader utilization increased.

Cheatgrass Quality

Cheatgrass was sampled only during 1996. Cheatgrass quality varied between winter ranges (P = 0.002) but not habitats (P = 0.298), and the range × habitat interaction was not significant (P = 0.661). Sampling date was not significant (P = 0.947); as with bitterbrush, cheatgrass quality did not vary temporally during our sampling period. Soil particle size (P = 0.680), soil depth (P = 0.700), and precipitation (P = 0.200) did not account for variation in the data and were removed from the analysis. Both aspect (P = 0.075) and slope (P = 0.096) were effective covariates by describing variation in the model and were retained in the analysis. Canonical 1 for winter ranges, driven by IVDMD, described 97% of the variation in the eigenvalue structure and was the only significant canonical. For IVDMD, cheatgrass in the Owyhee range had significantly higher digestibility than either the Bennett or Blacks Creek ranges, which were not different. Cheatgrass CP was virtually the same for the 3 winter ranges (Table 3).

Discussion

Bitterbrush Quality

Ammann et al. (1973) estimated that diets with 50% digestibility would meet the minimum maintenance requirement for a deer. Our estimates of bitterbrush IVDMD were considerably lower than 50% in all cases. This was expected based on previous winter estimates of bitterbrush IVDMD, which have ranged from 16.3 to 33.2% (Ward 1971, Urness et al. 1977, Welch and Pederson 1981, Welch et al. 1983a, 1983b, Welch and Wagstaff 1992). Our estimates of bitterbrush CP met the

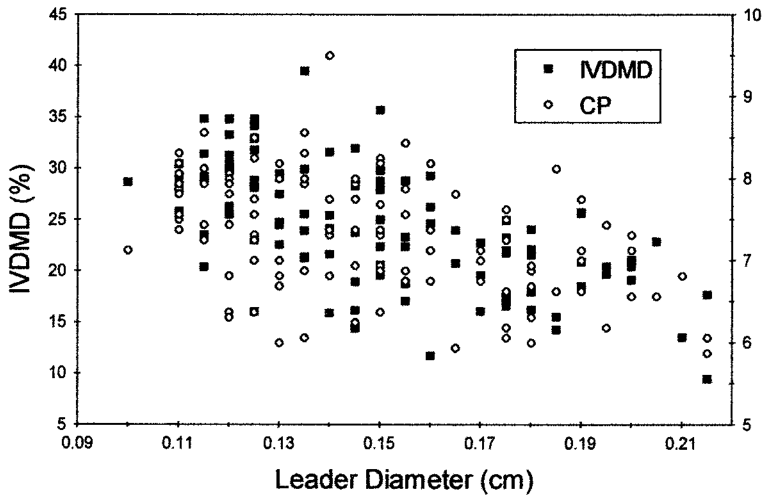

Fig. 3. Bitterbrush in vitro dry matter digestibility (IVDMD) and crude protein (CP) as a function of the diameter of available leaders among 3 mule deer winter ranges in southwest Idaho, 1997.

Table 3. **In vitro dry matter digestibility (IVDMD) and crude protein of cheatgrass for 3 mule deer winter ranges and 6 habitat components in southwest Idaho, 1996.**

Treatment	Class	IVDMD $\bar{x}$[1]	IVDMD SD	Crude Protein $\bar{x}$	Crude Protein SD
		------ (%) ------		------ (%) ------	
Winter Range	Bennett	67.3[a]	3.81	18.4	3.12
	Blacks Creek	65.8[a]	4.34	18.6	2.40
	Owyhee	69.6[b]	3.83	18.9	2.60
Habitat	High Shrub	67.0	5.00	18.9	3.10
	Low Shrub	67.0	2.78	17.3	2.30
	Scattered High Shrub	66.3	5.55	18.6	2.26
	Scattered Low Shrub	67.9	3.54	18.9	3.17
	Grass	68.0	4.25	19.2	3.31
	Riparian	69.3	3.81	18.6	1.64
Overall	Total Sample	67.6	4.27	18.6	2.70

[1]Within columns for each treatment, means with the same letter are not significantly different ($P > 0.05$). Letter superscripts are included only where post hoc mean comparisons were warranted.

approximate 5–7% minimum CP requirement for deer maintenance (Einarson 1946, Dietz 1965, Murphy and Coates 1966, Holter et al. 1979). Again, this was expected based on previous winter estimates of bitterbrush CP, which have ranged from 5.9 to 9.9% throughout the western U.S. (Bissell and Strong 1955, Dietz et al. 1962, Trout and Thiessen 1973, Tueller 1979). Although bitterbrush does not appear to meet the demands of mule deer, particularly in terms of digestibility, most available forage during the winter is nutritionally poor. In general, bitterbrush is considered an important shrub to wintering mule deer based on its palatability, ubiquity, relative quality, lack of essential oils (monoterpenoids), and the low availability of green forbs and grasses.

We found that bitterbrush quality, particularly IVDMD, varied among several deer winter ranges in southwest Idaho, and that quality decreased with increased utilization by deer and cattle. The Owyhee winter range had the highest bitterbrush quality both years. Of the 3 areas, it by far had the lowest mean deer density (1.3 ± 0.1 deer $km^{2\ -1}$). Conversely, the Bennett and Blacks Creek ranges had significantly lower overall quality yet supported greater mean deer densities (7.7 ± 0.2 deer km^{2-1} and 9.0 ± 0.4 deer km^{2-1}, respectively). The reported densities represent means for the entire winter ranges; deer densities in portions of the winter ranges were considerably higher. In 1997, we observed the least utilization on bitterbrush shrubs in the Owyhees, followed by the Bennetts, with the most utilization observed in Blacks Creek. This was consistent with the mean diameter of available leaders for each winter range, which was inversely related to bitterbrush quality (Fig. 4).

Given the low availability of shrub habitats across the Blacks Creek winter range, deer use of shrubs was heavily concentrated. We documented intense use of bitterbrush by measuring the diameter of available leaders. Large leader diameters, as a result of utilization, were directly correlated with poor bitterbrush quality in the Blacks Creek range (Fig. 4). The range fire in Blacks Creek not only reduced the quantity of shrubs, but also the quality (of bitterbrush) by concentrating use. During the 1996–97 winter, which is when we recorded leader diameters, weather conditions were average. In exceptionally harsh winters, deer have a greater reliance on shrubs, and the potential exists for extremely high deer mortality due to malnutrition, particularly for fawns. Similarly, fall drought conditions limiting growth of grasses may lead to high mortality when shrub cover is limited (Short 1981, Austin and Urness 1983, Urness et al. 1983).

The variation we observed in bitterbrush quality may be important for determining the nutritional quality of mule deer diets during winter. This is particularly true in southwest Idaho, where the variety of available forage is limited. In the Owyhee Mountains, 55 km south of our study area, Trout and Thiessen (1973) found that 97% of the February diets of mule deer consisted of bitterbrush, western juniper (*Juniperus scopulorum* Sarg.), and sagebrush. Given such low species diversity, site-specific variation in the nutritional quality of a single species could account for differences in diet quality among individual deer which seemingly do not exist based on the species composition of their diets.

Habitat explained some differences in bitterbrush CP, while precipitation, soil, and terrain variables accounted for minimal or no variation in bitterbrush IVDMD and CP. These factors likely contribute to regional differences in bitterbrush quality (i.e. one state to the next), where differences among various environmental variables are more pronounced. Genetic variation in bitterbrush likely exists at larger spatial scales as well (Welch et al. 1983a), probably as a result of differing climatic conditions and soil properties. Excluding differential browsing effects, intraspecies variation was apparently minor within the limited geographical extent of the deer winter ranges studied.

Cheatgrass Quality

Our estimates of cheatgrass IVDMD, which ranged from 65.8 to 69.6% across the winter ranges, were much greater than

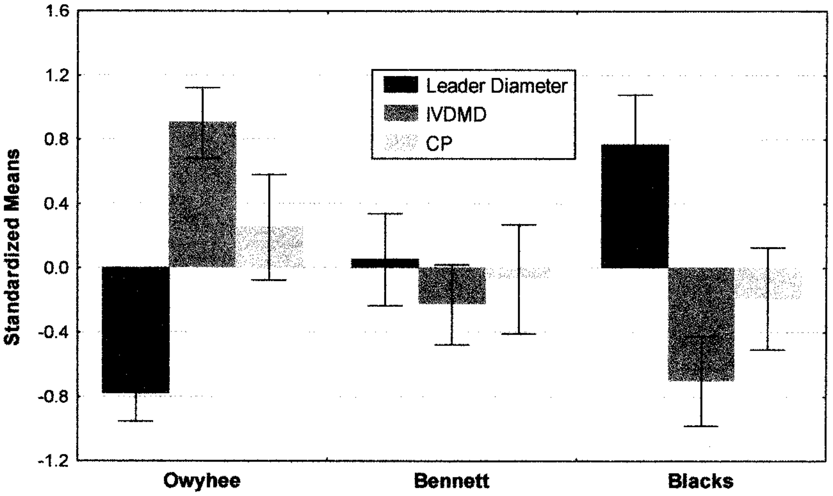

Fig. 4. Relative differences in bitterbrush leader diameter, in vitro dry matter digestibility (IVDMD), and crude protein (CP) among 3 mule deer winter ranges in southwest Idaho, 1997. The 95% confidence interval is shown for each standardized mean estimate.

the 50% minimum digestibility requirement for deer maintenance (Ammann et al. 1973). Austin et al. (1994) estimated cheatgrass in Utah to have 72.2% digestible dry matter. Given the high nutritional value of immature green grasses in general, the differences we found in cheatgrass digestibility probably have little biological relevance for mule deer. Our estimates of cheatgrass CP were nearly identical across the 3 winter ranges, which had a mean of 18.6%. A diet containing 16-17% CP is thought to meet the maximum needs of mule deer (Verme and Ullrey 1972). Previous protein estimates of green cheatgrass have ranged from 21.2% (Austin et al. 1994) to 25.6% (Dietz et al. 1962). Our nutritive values for cheatgrass verify the importance of green grass to wintering mule deer in southwest Idaho. Austin et al. (1994) evaluated the nutritional quality of 16 grasses found on deer winter ranges, all of which met or exceeded the nutritional requirements of deer. The timing and accessibility of green-up appears to be more critical for mule deer condition and survival than selection for particular grasses.

Conclusions

Future research evaluating mule deer habitat in terms of nutritional quality should consider site-specific nutritional variation within a single species along with interspecies differences, at least during winter when species diversity is limited. In our study, browsing pressure appeared to be the most important cause for observed differences in the nutritional quality of bitterbrush. Bitterbrush was the most nutritious in the Owyhee range, which had a low deer density. Higher deer densities coupled with fairly intense livestock grazing in places apparently reduced the quality of bitterbrush in the Blacks Creek and Bennett ranges. To improve habitat quality for deer in these and similar winter ranges, actions should be taken to promote shrub productivity and vigor while preventing excessive utilization of browse species prior to winter. Such actions include reseeding following natural or prescribed fire where appropriate shrub species are included in the seed mixture, and carefully managing the timing and intensity of grazing on winter range habitat.

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