



Lack of diet partitioning by sex in reintroduced desert bighorn sheep

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Desert bighorn sheep (*Ovis canadensis mexicana*) became extinct in Texas, U.S.A., during the 1960s and reintroduction efforts have resulted in an extant population of about 300 free-ranging animals. We studied diet preferences of reintroduced desert bighorn sheep in three mountain ranges in western Texas, U.S.A., during 1994–1995. We predicted that botanical composition and species richness of diets of reintroduced male and female desert bighorns differ when sexes are segregated, but are similar during portions of the year when sexes are aggregated. There were few consistent differences in diet composition between sexes. Species richness of diets of male bighorns was greater than for females. Forbs were highly preferred by both sexes but forb biomass was less than 1 kg ha⁻¹ in all seasons. Drought and impacts of historical livestock grazing on vegetation may have masked diet partitioning by sex.

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Introduction

Desert bighorn sheep (*Ovis canadensis mexicana*) are considered a relict species of the south-western United States, with documented range-wide declines resulting from a combination of poor competitive ability and adaptation to arid environments, and negative responses to anthropogenic changes such as livestock grazing and introductions of exotics (Bailey, 1980; McCutchen, 1981; Geist, 1985). Aesthetic, economic, and biodiversity concerns have led to conservation efforts aimed at restoring local and regional populations of desert bighorns.

Desert bighorn sheep historically inhabited as many as 16 mountain ranges west of the Pecos River in Texas, U.S.A. (Bailey, 1905). Texas bighorns declined sharply after 1900 due to disease, competition with livestock, and obstruction of movements by net-wire fencing, and became extinct in the 1960s (Davis & Taylor, 1939; Schmidly, 1977; Monson & Sumner, 1980). The Texas Parks and Wildlife Department began

efforts to restock bighorn sheep in Texas in 1957 and currently 300 free-ranging bighorns occur in several mountain ranges (Kilpatrick, 1991).

Desert bighorn sheep are sexually dimorphic and sexes segregate spatially outside the breeding, or aggregation, season. Hypotheses to explain sexual segregation in ungulates are manifold (Main & Coblentz, 1990; Miquelle *et al.*, 1992), with Main & Coblentz (1990) championing the idea that segregation results from differing reproductive strategies to maximize fitness. In the Mojave Desert of California, U.S.A., where segregation occurs from December to July, male bighorns exploited nutritionally superior habitats and selected diets of different botanical composition from females (Bleich *et al.*, 1997). Females exploit more rugged, often nutritionally inferior habitats to minimize predation of offspring (Festa-Bianchet, 1988; Berger, 1991; Bleich *et al.*, 1997). Miller and Gaud (1989) and Krausman *et al.* (1989) did not find pronounced differences in botanical composition of diets or habitat selection between male and female bighorns in the Sonoran Desert, Arizona, U.S.A. However, diets of male bighorns contained a higher percentage of forbs, the highest-quality food available, than diets of females in nearly all seasons and areas (Miller & Gaud, 1989).

Female bighorns in the Baylor, Beach, and Sierra Diablo mountains of western Texas use primarily higher, more rugged areas during the segregation period, whereas males are evenly distributed among elevations (DeYoung, 1997). Diet composition of males should differ from that of females during the segregation period if reintroduced desert bighorn sheep in western Texas exhibit similar foraging characteristics to desert bighorn sheep in their native habitat. Our objective was to determine the seasonal diet composition of reintroduced desert bighorn sheep in western Texas. We tested the hypothesis that reintroduced desert bighorns in western Texas differ in diet composition between sexes. We predicted that botanical composition and species richness of diets of male and female bighorns differ when sexes are segregated, but that diet composition and diet species richness of both sexes are similar during aggregation.

Materials and methods

Study area

The mountains of Trans-Pecos Texas are the foothills of the eastern Rocky Mountains, and lie within the Chihuahuan Desert biotic province. Soils vary considerably and include areas of shallow, rocky soils, and deep sands. Rainfall during 1993–1995 was 50–73% of the long-term average of 32.5 cm for Van Horn, Texas, the nearest town to our study areas (NOAA 1992–1995).

Our study areas included portions of the 84-km² Baylor Mountains (31.15°N; 104.47°W), the 46-km² Beach Mountains (31.7°N; 104.5°W) in Culberson county, and a 12-km² portion of the Sierra Diablo Mountains (Victorio Canyon) (31.2°N; 104.6°W) in Hudspeth and Culberson counties, Texas, U.S.A. Elevations range from 360 to 1960 m. Portions of the study areas were grazed by cattle in the flats and canyon bottoms. Warnock (1974) described the vegetation of the Baylor and Beach Mountains as a chino grama-lechuguilla (*Bouteloua breviseta* Vasey–*Agave lechuguilla* Torr.) association, and that of the Sierra Diablo Mountains as grassland with dense stands of pinon pine (*Pinus cembroides* Zucc.), Pinchot juniper (*Juniperus pinchotii* Sudw.), and oak (*Quercus* spp.).

Botanical composition of diets

We collected fresh fecal samples during spring (Mar.–May), summer (Jun.–Aug.), fall (Sep.–Nov.), and winter (Dec.–Feb.) months for 2 years (1994–1995) from bighorns in

the Beach, Baylor, and the Sierra Diablo Mountains. Fecal samples were collected following observed defecation from male and female bighorns. Animals were allowed to move from the site of defecation before feces were collected to avoid harassment. We attempted to collect 20 fecal groups (>10 fecal pellets in a 25-cm radius) for each season-area-sex combination for each year. Feces were placed in sterile plastic bags, stored on ice, and frozen within 24 h. Samples were then freeze-dried and ground in a Wiley mill through a 1-mm mesh screen. A 1-g subsample was taken from each fecal sample. Sub-samples from each sex-site-season combination were combined into a composite sample and sent to a professional laboratory with experience at determining bighorn diets (Fecal Analysis Laboratory, University of Arizona, Tucson, U.S.A.) for microhistological analysis (Sparks & Malechek, 1968; Krausman *et al.*, 1989). For each sex-site-season composite, five slides and 20 fields per slide were examined for plant fragments.

Forage standing crop

We established sites for vegetation sampling by delineating areas where desert bighorns were observed in each study area on a map and randomly selecting four sites in each mountain range. At each site, we established permanent 100-m vegetation transects in a stratified, random manner. Transects were proportionally located by slope, aspect, and elevation. We divided each site into three elevation strata: upper, middle, and lower slopes. In a site, five transects were sampled within each of the three strata during spring, and three transects were sampled within each of the three strata in all other seasons. Plots measuring 0.5 m² by 1.5 m were placed at 10-m intervals along each transect. Plant species that composed greater than 1% of bighorn diets in 1994 were considered forage species during sampling.

In 1995, we estimated biomass of forage species with a double-sampling technique (Bonham, 1989) each season. Vegetation sampling coincided with fecal sampling (Mar.–May, Jun.–Aug., Sep.–Nov., and Dec.–Feb.). Forages within each plot were clipped at a 3 : 10 ratio of clipped to estimated plots during spring and at a 4 : 10 ratio in all other seasons. Clipped forages, which included leaves and stems of herbaceous plants and leaves and nonlignified twig tips of woody plants, were separated by species and weighed in the field. Clipped samples were later air-dried and reweighed. Subsamples were oven-dried at 105°C for 24 h to determine dry mass. Individual plots were not sampled more than once. A total of 600 plots per mountain range were sampled in spring, and 360 plots per mountain range per season were sampled thereafter.

Wet weights of forage species were converted to dry mass with a ratio estimator of wet : dry matter for each species for each season-area combination. Forage species that were estimated but not clipped were converted to dry matter using a wet : dry matter ratio by forage class (i.e. browse, forbs, grass, succulents) for each season-area combination.

Statistical analyses

Data on percent relative density of forbs, grasses, browse, succulents, and 10 individual plant species that composed greater than 3% of sheep diets were averaged across years and across December, March, and June sampling dates to represent the period of segregation. September data were pooled across years and represented the period of aggregation. These dates were chosen based on field observations (Robbins & DeYoung, unpublished data) and to coincide with periods of segregation and aggregation documented by Bleich *et al.* (1997). Sample sizes for species that composed less than 3% of diets were inadequate for statistical analyses.

Diet data (relative density of forbs, grass, browse, succulents, and key species) were compared by analysis of variance for a randomized, complete block design with mountain ranges as blocks (replicates) (SAS Institute, Inc., 1989). Period (aggregation *vs.* segregation) and sex (ram *vs.* ewe) were main effects with period \times sex as the interaction term. Species richness (number of different species in the diet) was also compared by analysis of variance with period and sex as main effects and period \times sex as the interaction term.

Standing crop (kg ha^{-1}) of bighorn sheep forage species composing greater than 1 kg ha^{-1} of the available forage was compared by analysis of variance for a randomized, complete block design with mountain ranges as blocks (replicates). Period (aggregation, segregation) and slope position (low, mid, and high) were main effects and period \times slope was the interaction term.

Preference for forage classes (browse, forbs, grasses, or succulents) was evaluated using the forage ratio (p) of a sex for a given forage class c (Loehle & Rittenhouse, 1982; Negi *et al.*, 1993)

$$p_c = H_c/D_c$$

where H is the percent relative density of forage class c in the diet and D is percent of forage class c in the phytomass. Preference also was evaluated with the electivity index E for each forage class (Ivlev, 1961):

$$E_c = (D_c - H_c)/(D_c + H_c)$$

Indices were calculated with data pooled across sexes for Dec.–Feb., Jun.–Aug., and Sep.–Nov. 1995.

Results

Bighorns used 35 total plant genera including 14 shrubs, 12 forbs, and nine grasses. *Eriogonum* spp. and *Sphaeralcea* spp. were the two major forbs in diets. The sampling period \times sex interaction ($F = 10.41$; 1, 6 df.; $p = 0.018$) varied for relative density of *Sphaeralcea* spp. in diets, with females consuming more than males during the period of aggregation (Table 1). Across sampling periods, females ($\bar{x} = 1$, S.D. = 2%) ate less ($F = 6.70$; 1, 6 df.; $p = 0.0413$) cloak fern (*Notholeana* spp.) than males ($\bar{x} = 5$, S.D. = 3%). Main and interaction effects were not significant ($p > 0.05$) for the other eight species that constituted greater than 3% of the diets.

Relative density of grass, forbs, browse and succulents in bighorn diets did not differ ($p > 0.05$) between sampling periods, between sexes, or for the sex \times sampling period interaction. Grasses, forbs, browse, and succulents averaged ($\bar{x} \pm$ S.D.) 16 ± 10 , 40 ± 6 , 36 ± 7 , and $8 \pm 4\%$ for males and 16 ± 7 , 44 ± 9 , 33 ± 5 , and $7 \pm 4\%$ for females, respectively.

There was no sex \times sampling period interaction for species richness in the diet ($F = 0.10$; 1, 6 df.; $p = 0.76$). There were main effects of sampling period ($F = 39.41$; 1, 6 df.; $p = 0.001$) and sex ($F = 8.25$; 1, 6 df.; $p = 0.028$). Females ate fewer ($\bar{x} = 18$, S.D. = 7%) food items than males ($\bar{x} = 23$, S.D. = 6%). During the period of segregation, desert bighorns consumed more food items ($\bar{x} = 26$, S.D. = 5%) than during aggregation ($\bar{x} = 16$, S.D. = 3%).

Total biomass of forage species eaten by desert bighorns did not differ ($F = 1.93$; 2, 10 df.; $p = 0.195$) among slope locations (Table 2). However, biomass of desert bighorn forages was greater ($F = 7.62$; 1, 10 df.; $p = 0.020$) during seasons when males and females were segregated than during aggregation.

Prickly pear cladophylls composed the bulk of forage available in all mountain ranges during all seasons. Grasses were the second major forage class available, with grama

Table 1. Percentage ($n = 3$) of the 10 most utilized plant genera or species in the diets of desert bighorn sheep during the period of segregation (winter, spring, summer) and aggregation (fall), Beach, Baylor, and Sierra Diablo Mountains, Texas, U.S.A., 1994–1995

Genus or species	Segregation				Aggregation				p -value*
	Male		Female		Male		Female		
	\bar{x}	S.D.	\bar{x}	S.D.	\bar{x}	S.D.	\bar{x}	S.D.	
Browse									
<i>Artemisia</i> spp.	8	1	9	4	15	2	7	9	0.206
<i>Cercocarpus montanus</i>	3	2	1	1	5	1	7	8	0.448
<i>Prosopis glandulosa</i>	3	3	7	5	4	5	3	3	0.440
<i>Rhus</i> spp.	6	2	5	5	4	4	8	6	0.402
Forbs									
<i>Eriogonum</i> spp.	19	4	21	2	16	1	21	8	0.566
<i>Krameria</i> spp.	5	3	3	3	3	1	1	1	0.741
<i>Notholeana</i> spp.	5	1	1	1	5	4	1	2	0.938
<i>Sphaeralcea</i> spp.	12	3	10	1	10	4	22	7	0.018
Grasses									
<i>Bouteloua</i> spp.	5	1	7	3	11	7	9	4	0.360
Succulents									
<i>Opuntia</i> spp. (pad)	6	1	7	2	7	4	2	2	0.111

* p -value for the sex \times sampling period interaction.

grasses (including sideoats grama, *Bouteloua curtipendula* (Michx.) Torr., black grama, *B. eriopoda* (Torr.) Torr., blue grama, *B. gracilis* (Kunth in H.B.K.) Lag. ex Griffiths, and hairy grama, *B. hirsuta* Lag.) composing the greatest percentage of grass biomass during all seasons. Mormon tea was the most abundant browse species. Forbs, including wild buckwheat, were available only in trace amounts (<1%; Table 2).

Based on the forage ratio and electivity indices, forbs were highly preferred over other forage classes (Table 3). Browse was second in preference to forbs. Grasses and succulents were avoided based on the electivity index.

We observed sheep eating several species that were not detected in microhistological analysis, including yellow trumpet flower (*Tecoma stans* (L.) Juss. ex Kunth in H.B.K.), ocotillo (*Fouquieria splendens* Engelm.), and mammillaria cactus (*Mammillaria* spp.). Desert bighorn sheep in our study areas used several genera that were not encountered in vegetation sampling. These included sagebrush (*Artemisia* spp.), Janusia (*Janusia* spp.), and beard-tongue (*Penstemon* spp.).

Discussion

The paucity of forbs in the habitat compared to the relatively large amount of forbs in the diets indicated that forbs were more highly preferred by desert bighorn sheep in the Beach, Baylor, and Sierra Diablo Mountains than grasses, browse, or succulents. Grasses composed 62–81% of desert bighorn sheep diets in Nevada (Brown *et al.*, 1977). Browse dominated desert bighorn diets in Arizona and New Mexico (Barrett, 1964; Monson & Sumner, 1980; Krausman *et al.*, 1989; Miller & Gaud, 1989). The flexibility in diet preference exhibited by desert bighorn sheep is advantageous in desert

Table 2. Standing crop (kg ha^{-1}) of plant species eaten by desert bighorn sheep during the period of segregation (winter, spring, summer) and aggregation (fall), Beach, Baylor, and Sierra Diablo Mountains, Texas, U.S.A., 1995

Genus	Segregation		Aggregation		<i>p</i> -value
	\bar{x}	S.D.	\bar{x}	S.D.	
Browse					
<i>Acacia</i>	< 1	< 1	< 1	< 1	
<i>Cercocarpus montanus</i>	< 1	1	< 1	< 1	
<i>Dalea</i>	< 1	< 1	< 1	< 1	
<i>Ephedra</i>	18	12	7	6	0.058
<i>Euphorbia</i>	< 1	< 1	0	0	
<i>Fallugia</i>	< 1	< 1	< 1	< 1	
<i>Fraxinus</i>	< 1	< 1	0	0	
<i>Krameria</i>	< 1	< 1	0	0	
<i>Quercus</i>	1	1	< 1	< 1	0.083
<i>Rhus</i>	< 1	< 1	< 1	< 1	
Forbs					
<i>Allium</i>	< 1	< 1	< 1	< 1	
<i>Eriogonum</i>	< 1	< 1	< 1	< 1	
<i>Sphaeralcea</i>	< 1	< 1	0	0	
Grasses					
<i>Aristida</i>	4	2	3	1	0.218
<i>Bouteloua</i>	29	18	21	15	0.117
<i>Bromus</i>	< 1	< 1	< 1	< 1	
<i>Muhlenbergia</i>	10	11	7	8	0.316
Succulents					
<i>Opuntia</i> (pads)	117	56	77	43	0.070
Total	180	64	114	52	0.020

habitats where nutritional quality and availability of different forage classes varies with wet and dry periods (Miller & Gaud, 1989). Bighorns may select forages that, based on trade-offs in forage biomass or nutritional quality, allow them to maintain nitrogen balance (Hobbs *et al.*, 1982). In our study, the nitrogen content of forbs was 2–3 times greater than the nitrogen content of browse (DeYoung *et al.*, 2000). The greater nitrogen of forbs may explain the strong preference for forbs by desert bighorn sheep in western Texas.

Eriogonum spp. and *Sphaeralcea* spp. appear to be important genera in the diets of desert bighorn sheep in the Sonoran and Chihuahuan Deserts. Although browse dominated diets in the study of Krausman *et al.* (1989), percentages of *Eriogonum* spp. and *Sphaeralcea* spp. in bighorn diets in the Sonoran Desert were similar to those found in our study in the Chihuahuan Desert. Abundance and biomass of these genera should be included in habitat suitability models used to assess habitat for transplanting desert bighorn sheep.

Our results did not support the prediction that botanical composition and species richness of diets of male and female bighorns differ when sexes are spatially segregated, but are similar for both sexes during aggregation. Our failure to observe diet partitioning by sex resulted from low forage production. We predicted that diets of females differ from males during segregation because females utilize higher, more rugged habitats during segregation. The higher, more rugged habitats were expected to have

Table 3. Forage ratio (\pm S.D.) and electivity index (\pm S.D.) of browse, forbs, grasses, and succulents in desert bighorn sheep diets in western Texas, U.S.A., 1994–1995

Index and lifeform		Sampling date		
		Winter 1995 <i>n</i> = 4	Summer 1995 <i>n</i> = 6	Fall 1995 <i>n</i> = 6
Forage ratio				
Browse	\bar{x}	3	3	4
	S.D.	1	1	1
Forbs	\bar{x}	2068	2525	734
	S.D.	542	544	287
Grasses	\bar{x}	< 1	< 1	< 1
	S.D.	< 1	< 1	< 1
Succulents	\bar{x}	< 1	< 1	< 1
	S.D.	< 1	< 1	< 1
Electivity index				
Browse	\bar{x}	0.74	0.34	0.56
	S.D.	0.31	0.30	0.11
Forbs	\bar{x}	1.0	1.0	1.0
	S.D.	< 0.01	< 0.01	< 0.01
Grasses	\bar{x}	− 0.45	− 0.70	− 0.49
	S.D.	0.39	0.46	0.29
Succulents	\bar{x}	− 0.71	− 0.75	− 0.86
	S.D.	0.09	0.18	0.11

lower quality and quantity of forage. However, biomass of forbs (less than 1 kg ha^{−1}) and other key forages eaten by bighorns was low throughout the study area and did not differ between lower slopes and the more rugged habitats of the upper slopes of the mountains. Biomass of preferred forages was so low that differential forage preference by males and females may have been too muted to observe.

Male desert bighorns have a greater absolute nutrient requirement than females because their body mass is twice that of females. Bighorn sheep continually sample available forages to gain information about forage quality, which helps them to maintain consistent nutrition when nutrients are in short supply (Miller & Gaud, 1989). Forage sampling was possibly more pronounced for males in our study since males consumed a wider range of genera than females. Males may have sampled a wider range of forage species because of their greater absolute nutrient requirement coupled with the scarcity of high-quality forage in the study area.

Below-average rainfall during our study and grazing by domestic sheep during the first half of the 20th century may be responsible for low forb production and the lack of sexual partitioning in diet on the study area. Diet preferences of desert bighorns that originally inhabited the study areas and pre-extinction botanical composition of the areas are unknown. Although it would be difficult or impossible to document, it is possible that changes in composition of vegetation have occurred coincident with European settlement that have reduced the abundance of plants eaten by desert bighorns. Records indicate that before 1930, domestic sheep numbered < 3500 annually within Culberson and Hudspeth counties (*Texas Almanac*, 1928). However, in 1940, domestic sheep numbers reached 74,000, and exceeded 100,000 by 1945 (*Texas Almanac*, 1947). The huge buildup in sheep densities in the 1940s possibly resulted in

long-term adverse impacts to bighorn sheep habitat in the region through depletion of preferred forage species.

Vegetation recovery in arid habitats following intense disturbance such as overgrazing is extremely slow. Once vegetation composition is pushed across a certain threshold, traditional successional trends back to a plant composition that previously existed may not occur (Laycock, 1991). Suitable habitat for male bighorns may be particularly impacted by grazing, because they are more likely than females to use areas grazed by cattle (i.e. less rugged areas; Bleich *et al.*, 1997).

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