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Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*)

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Abstract

Dramatic declines in the endangered Columbia Basin pygmy rabbit, a genetically unique population of small, burrowing rabbits in Northwestern United States, are likely the combined results of habitat degradation and fragmentation, disease, and predation. A critical component of pygmy rabbit habitat includes big sagebrush (*Artemisia tridentata*), which constitutes 82–99% of their winter diet and 10–50% of their summer diet. Sagebrush also forms the bulk of hiding cover around burrow sites. Across the range of pygmy rabbits, sagebrush habitat is grazed extensively by cattle. However, grazing has unknown effects on pygmy rabbits inhabiting the remaining, fragmented shrub-steppe habitat. We evaluated the effects of four grazing treatments on the distribution of pygmy rabbit burrows, diets of pygmy rabbits, and quality and quantity of vegetation at Sagebrush Flat in central Washington. Ungrazed areas contained significantly more burrows per unit area than did grazed areas. Vegetation composition and structure differed little among treatments in early summer before annual grazing by cattle. However, cattle grazing in late summer through winter removed about 50% of the grass cover, and reduced the nutritional quality (e.g., increased fiber and decreased protein) of the remaining grass. Although pygmy rabbits ate <2% grasses in winter, grasses and forbs comprised 53% of late summer diets. Because these endangered rabbits avoided grazed areas, removing cattle grazing from key habitat locations may benefit efforts to restore this rabbit in Washington.

Author Keywords: Cattle grazing; Columbia Basin; Habitat selection; Pygmy rabbits ; Sagebrush

Article Outline

1. Introduction

Lagomorphs are known for their high fecundity, yet many species of rabbits worldwide have been placed on The World Conservation Union's (IUCN) Red List of Threatened Species (Lagomorph Specialist Group, 1996). In North America, six species of rabbits are classified as Endangered by IUCN and/or United States Fish and Wildlife Service (USFWS), including Dice's cottontail (*Sylvilagus dicei*) of central America, Volcano rabbit (*Romerolagus diazi*) and Tres Marias rabbit (*Sylvilagus graysoni*) of Mexico, Lower Keys rabbit (*Sylvilagus palustris hefneri*) of Florida, Riparian Brush rabbit (*Sylvilagus bachmani riparius*) of California, and most recently (February 2003), the Columbia Basin pygmy rabbit (*Brachylagus idahoensis*) of central Washington, USA. As of 2003, fewer than 30 pygmy rabbits were estimated to remain in their natural sagebrush-steppe habitat in central Washington, and an intensive captive breeding and release program is underway as a last-ditch effort to save this distinct population segment (Oregon Zoo, 2001).

Pygmy rabbits are one of the smallest lagomorphs in the world (450 g) and one of only two North American rabbits that dig their own burrows. The other species, the volcano rabbit, is similarly endangered and inhabits diminishing open pine forests growing on deep soils in Mexico (Lagomorph Specialist Group, 1996). Pygmy rabbits are uniquely dependent on big sagebrush (*Artemisia tridentata*) for cover and food, occupying some of the remaining sagebrush steppe of the Great Basin where sagebrush is relatively tall and dense and soils are deep (Gahr, 1993; Gabler, 1997; Green and Flinders, 1980; Weiss and Verts, 1984). Deep soils allow pygmy rabbits to dig burrow systems (Wilde, 1978; Weiss and Verts, 1984) and dense sagebrush provides a valuable winter food source, thermal cover, and protection from predators (Katzner and Parker,

1997; Katzner et al., 1997; Wilde, 1978; Green and Flinders, 1980). Pygmy rabbits subsist almost exclusively on sagebrush in the winter, and even in the summer when grass and forbs are available, sagebrush forms up to 50% of their diet (Green and Flinders, 1980).

Archeological evidence suggests that Washington's Columbia Basin pygmy rabbit has been separated from the rest of the species' range in Idaho, Montana, Oregon, and surrounding Great Basin states for at least 4000–7000 years, when climate changes caused the distribution of sagebrush to contract (Lyman, 1991; Grayson, 1987). Museum records and sightings indicate that pygmy rabbits at one time inhabited five counties in central Washington, but these populations have declined rapidly over recent decades (McAllister, 1995; Musser and McCall, 2000). By 2000, fewer than 100 animals remained in a single population at Sagebrush Flat (SBF), a 1311 ha area of sagebrush habitat in Central Washington owned by Washington Department of Fish and Wildlife (WDFW). Recent analyses have shown that this Washington population is genetically distinct, distantly related to populations in nearby states, and have likely been separated from other populations for >40,000 years (Warheit, 2001).

The conversion and degradation of suitable habitat has likely been the primary cause of severe declines in pygmy rabbits in the Columbia Basin over the last 5 decades and most of the remaining sagebrush-steppe in the Columbia Basin and neighboring states have provided or continue to provide ranchers with valuable lands for grazing of livestock. The effects of livestock grazing on habitat suitability for pygmy rabbits, however, are not well known. In theory, cattle grazing may either reduce or enhance habitat for pygmy rabbits depending on its intensity and season. Intensive cattle grazing in sagebrush steppe can reduce grass and forb cover and increase height and density of sagebrush (Laycock, 1991; Daubenmire, 1988; Bennett, 1999). Because pygmy rabbits typically select core areas where sagebrush is taller and denser within their small home ranges (≈0.30 ha, McAllister, 1995; Gahr, 1993; Gabler, 1997; Green and Flinders, 1980; Weiss and Verts, 1984), grazing may promote habitat conditions sought after by pygmy rabbits. If grazing occurs in late spring, cattle can increase the nutritional quality of grasses by sustaining regrowth and retarding lignification that occurs with aging (Clark et al., 2000; Wambolt et al., 1997; Van Soest, 1994). However, grazing can also reduce the cover of grasses and forbs, likely a critical component of a pygmy rabbit's diet in spring and summer, either directly by consumption or indirectly by altering species composition and succession of the plant community (Fleischner, 1994; Knick, 1999; Laycock, 1991). Large herbivores like cattle may also reduce the regeneration of sagebrush by tearing the root systems and trampling emerging plants (Owens and Norton, 1990).

To manage areas in which pygmy rabbits currently reside and select the best sites for future reintroduction efforts, we must increase our understanding of the ecological implications of cattle grazing on pygmy rabbits and their habitat. To do so, we compared grazed and ungrazed areas of SBF for differences in pygmy rabbit burrow distribution, habitat components, nutritional quality of forages, and finally rabbit diet composition.

2. Methods

2.1. Study area

We examined cattle grazing and pygmy rabbit habitat at SBF in central Washington in 1996 and 2000. The 1311-ha area has an overall southern aspect and ranges in elevation from 488 to 579 m. Temperatures range from □3 to 38 °C, and the average annual precipitation is 20 cm. Soils at SBF are deep with a sandy loam texture. The overstory vegetation at SBF is dominated by big sagebrush (*A. tridentata*) with an understory cover of native grasses and forbs. The area is inhabited by many animals associated with declining sagebrush steppe, such as sage grouse (*Centrocercus urophasianus*), white-tailed jackrabbit (*Lepus townsendi*), and Washington ground squirrel (*Spermophilus washingtoni*).

In 1993, private landowners and state and federal agencies developed a grazing plan for SBF, dividing it into four units and subjecting it to different grazing treatments (Guinn, 1993, Fig. 1). Unit 1 consisted of 366 ha in the east central part of the study area and was grazed during the dormant season for grass (from 16 June to 29 February). Unit 1A, west central, consisted of 186 ha that was grazed before 1997, and thereafter was excluded from grazing. The northern most unit, Unit 2, consisted of 454 ha which was grazed for 3 years followed by 1 year of rest. The remaining 305 ha in the south (Unit 3) had not been grazed since 1957. Although two of the treatments were grazed during the period of our study and 2 were ungrazed, this design of grazing treatments (including a rare 40-year exclosure) at SBF included no exact replicates, a common limitation of long-term exclosure experiments (Brown and McDonald, 1995; van Mantgem et al., 1991.) This design does not allow us to generalize about the effects of cattle grazing on pygmy rabbits and their habitats in other areas, nor to establish grazing, rather than potential confounding environmental factors, as the definitive cause of patterns seen at SBF. Nevertheless, even a single replicate of important ecosystem and population-level phenomena represents a valuable, and perhaps a final, opportunity to gain information about such a critically endangered population (Sinclair, 1991; Eberhardt and Thomas, 1991).

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Fig. 1. Shaded areas within western United States represents current range of pygmy rabbits. Star in central Washington marks remaining location of Columbia Basin pygmy rabbits in Washington and the study site Sagebrush Flat. Inset shows grazing units and Columbia Basin pygmy rabbit (*Brachylagus idahoensis*) burrow locations from a comprehensive survey at Sagebrush Flat, Washington, during summer and fall of 2000. Unit 2 (grazed according to House Bill 1309), 1 (grazed during the dormant growth period), 1A (grazed before 1997), and unit 3 (not used or fenced since 1957).

2.2. Burrow activity and location

From July through September 2000, we conducted a complete search of SBF to locate all pygmy rabbit burrows. We walked belt transects with 3–20 m between observers depending on the density of the vegetation. Universal transverse mercator (UTM) coordinates were recorded for all pygmy rabbit burrows using a hand-held GPS unit and the burrow was classified as active or inactive. A burrow was classified active if the rabbit pellets appeared to be less than 2 weeks old. We determined age by observing pellets of a known age, in wet and dry conditions, and monitoring how the shine, color, and shape changed during a 2-week period. When rechecking activity at burrows from July through September, pellets were swept away to make subsequent rechecks easier and more consistent. Through September we rechecked all burrows biweekly to determine changes in activity. We returned 3 times to determine which burrows were currently being used by pygmy rabbits.

During rechecks of burrows, we recorded whether cottontail rabbits (*Sylvilagus* spp.), which do not dig their own burrows, were using a pygmy rabbit burrow by noting a sighting, tracks, or pellets. Fecal pellets from cottontail rabbits were distinguished from pygmy rabbit pellets by their size and shape. Pygmy rabbit pellets average 4–5 mm and are consistent in size and shape, whereas cottontail pellets average 7–8 mm and can vary in size.

We used a χ^2 goodness-of-fit test (Alldredge and Ratti, 1992) to determine significant differences in the total number of burrows in each grazing unit and among the 2 grazed and 2 ungrazed units. We then used the Bonferroni *z*-statistic (Alldredge and Ratti, 1992) to determine which units had significantly more or fewer burrows than expected. Expected occurrence was based on the available area of each grazing unit. χ^2 goodness-of-fit tests were also used to determine differences in activity of pygmy rabbit burrows and of cottontail use of pygmy rabbit burrows among units during summer and winter.

2.3. Diet composition of pygmy rabbits

To determine whether food habits of pygmy rabbits differed among grazing units, we collected fresh faeces from all active burrow sites during August and December 2000. One pellet group was collected at each burrow and represented an individual sample. We used microhistological analyses of faeces, commonly used for herbivores, as an index of rabbit diets (Matrai et al., 1998; Chapuis et al., 1985). Samples were prepared and stained using methods of Davitt and Nelson (1980) and botanical composition of all diets was determined by the Wildlife Habitat Lab at Washington State University (Pullman, WA) using a total of 150 microscope views per sample. Percent diet was determined of major genus of all grasses, forbs, and shrubs. Big sagebrush components were further separated into stems, leaves, and flowering parts. Diet composition was compared between grazed and ungrazed areas using analysis of variance on arcsin-transformed data.

Preference of shrubs, grasses, and forbs by pygmy rabbits was determined for grazed and ungrazed areas during the summer before annual grazing using the Friedman test and multiple comparisons (Conover, 1980). Percent use of individual diets (grazed areas

n=10, ungrazed areas *n*=8) was compared to percent availability of forage categories taken from the habitat measurements determined for each plant category.

2.4. Composition and structure of vegetation

To compare habitat features among grazing units at SBF, we first compared species composition and cover of >90 plant species, and the density, height, and age class distribution of sagebrush in summer before annual grazing. We measured vegetation on 103 randomly selected 1-ha plots in June 1996 and 2000. To characterize species composition and cover, we used the metric belt transect system with a 0.1 m frame (Schmutz et al., 1982). The point-centered quarter method (Bonham, 1989) was used to describe age class distribution, height, height to first live material, and density of sagebrush at the plots. We estimated age class of sagebrush based on height, and percent of living material and reproductive state. Sagebrush plants were assigned one of six age classes: (1) immature seedlings under 5 cm; (2) young plants under 10 cm that are not producing the maximum amount of seeds; (3) mature plants with little or no decadent material; (4) plants <25% decadent; (5) plants 25–50% decadent; and (6) plants >50% decadent.

To determine if vegetation characteristics differed among the four units and between the two years, we used analysis of variance, with year and unit categories as independent variables, sagebrush density and height and canopy cover of individual species and vegetative groups as dependent variables, and year*unit as the interaction term (PROC GLM, SAS Institute, Inc., 1985). We used an arcsin transformation on percent canopy cover before analyses, except for total plant cover, which can sum to over 100%.

Utilization of grasses by cattle was monitored between 1996 and 2000 by WDFW and measured in animal unit months (AUMs) or the amount of forage needed to feed one cow, or its equivalent, for one month. SBF Managers also measured a combined use of bluebunch wheatgrass and Thurber's needlegrass for the 2 grazed units using Natural Resources Conservation Service (NRCS, 1997) protocol for determining percentage of grazed plants. The percent removal by weight of 300 measurements for both species in each unit was compared to baseline data created pre-grazing.

2.5. Nutritional quality of pygmy rabbit forages

To compare nutritional quality of common forages eaten by pygmy rabbits among grazing units, we collected samples of bluebunch wheatgrass, needlegrass, big sagebrush, and rabbitbrush (*Chrysothamnus* spp.) in June and December 2000, and March 2001 from 10 randomly selected plots in each unit where vegetation measurements had been taken. In June and March, the sagebrush was separated into two categories: immature plants (age classes 1–2) and mature plants <50% decadent (age classes 3–5). In December, the young plants (usually <12 cm) were under snow, thus we collected only from the mature plants above snow level. From both shrub species, we collected samples of the current year's growth. Leaving 2.5-cm stubble, we collected all material (dead and alive) available from the grasses.

We determined fiber composition of forage using a sequential detergent analysis (Goering and Van Soest, 1970) with filter bags, sodium sulfite, and alpha-amylase in an Ankom Fiber Analyzer (Ankom Technology, Fairport, NY). Crude protein was determined by the Kjeldahl procedure (Bradstreet, 1965). We determined differences in fiber composition and crude protein among units and seasons with year*grazing as the interaction term in SAS, on arcsin-transformed data (SAS Institute, Inc., 1985).

2.6. Other habitat features

To compare aspect, slope, and soil type and depth among grazing units and at pygmy rabbit burrows, we used GIS mapping and overlay with ARC/VIEW and ARC/INFO software (Environmental Systems Research Institute, Redlands, California, USA). Using a United States Geological Survey (USGS) 30 m Digital Elevation Model, we developed a separate slope and aspect layer. The slope layer described percent slope in six consecutive categories: 0–5%, 5–10%, 10–15%, 15–20%, 20–30%, and 30% and up. The aspect layer described all major slope directions: Flat, N, NE, E, SE, S, SW, W, and NW. The digitized soils map was created by NRCS as a polygon coverage of major soil type complexes in Douglas County and at the time only a draft coverage was available. The soil layer was also used to create a polygon coverage describing soil depth in categories; 17.5–25, 25–50, 50–100, 100–150, and >150 cm, using depths from Kehne (1991). Within a polygon, two or more soil types with varying depths could occur. The shallowest soil depth was used to describe the entire polygon. All four layers were clipped in ARC/VIEW using a layer that outlined the units of SBF created by digitizing an aerial photo of the study site. The last layer was a point vector file of burrow locations in 2000 with attribute data on activity and cottontail use of pygmy rabbit burrows.

The point file of burrows was separately overlain on the aspect, slope, soil types, and soil depth layers to characterize each burrow. From each layer (soil type and depth, aspect, aspect slope), we also determined the percent area of each individual category making up that layer. We projected the expected number of burrows in each category based on percent area. Knowing expected and observed number of burrows in each category, we used the Neu Method of the χ^2 goodness-of-fit test (Alldredge and Ratti, 1992) to determine if there were significantly more or fewer burrows than expected in each descriptive category based on availability. The χ^2 test for homogeneity and Bonferroni *z*-statistic were used to determine differences in distribution of habitat characteristics (soil type and depth, aspect, and slope) among grazing units.

3. Results

3.1. Burrow activity and location

We found 165 pygmy rabbit burrows within SBF during the summer and fall of 2000 (Fig. 1). The percent of active burrows declined from 31% to 22% from summer to winter. During the summer (χ^2=25.26, DF=1, p<0.001) and winter (χ^2=29.92, DF=1, p<0.001), we found significantly more active burrows in ungrazed units than units grazed by cattle. In March 2001, only one of the original 165 burrows was active, reflecting

empirical observations of a large population decline. After the breeding season in June 2001, 9 burrows were active. Cottontails used 12% (n=20) of available pygmy rabbit burrows across SBF during winter and used burrows only in the grazed areas. During the winter, significantly more pygmy rabbit burrows were used by cottontails in grazed than ungrazed units (χ^2=22.87, DF=1, p<0.001), and no cottontail sign was found at pygmy rabbit burrows in ungrazed areas.

During weekly rechecks in the summer, burrows changed in activity category from one week to the next. From the first week to the second week of August 2000, 25% of the burrows changed in activity, and of those, 61% changed from inactive to active. Therefore, all pygmy rabbit burrows were used for analyses of habitat use among grazing units, regardless of whether they were classified as active or inactive. Using all burrows, the 4 units at SBF were not used by pygmy rabbits in proportion to availability (χ^2=72.83, DF=3, p=0.0001). Unit 3, which remained ungrazed since 1957, had the highest burrow density (0.26 burrows/ha) and significantly more burrows than expected based on area (p<0.05), whereas Unit 1A (0.03 burrows/ha), grazed before 1997, and Unit 1 (0.07 burrows/ha), grazed during the dormant growth period, both had significantly fewer than expected (p<0.05). Only Unit 2 with 0.17 burrows/ha and grazed according to ecosystem standards set by the State of Washington legislature was used in proportion to availability (p>0.05) based on the Bonferroni z test. When the two grazed units (Units 1 and 2) and ungrazed units (Units 1A and 3) were combined, significantly more burrows than expected were found in ungrazed habitats at SBF in 2000 (χ^2=17.58, DF=1, p=0.0001).

3.2. Diet composition of pygmy rabbits

Grasses and forbs formed the bulk of pygmy rabbit diets in the summer, especially the genera *Agropyron*, *Koeleria*, *Poa*, *Achillea*, *Astragalus*, and *Lupinus* (Table 1, for a complete list see Appendix C, Siegel, 2002). In winter, pygmy rabbits consumed big sagebrush virtually exclusively, with a small amount of rabbitbrush (*Chrysothamnus* spp.) and *Bromus tectorum*. Rabbits ate more shrubs and less grasses and forbs in the winter (all p<0.0001, Table 1). However, a similar proportion of their diet consisted of

shrubs, grasses, and forbs in grazed and ungrazed areas (all p 0.4242, Table 1).

Table 1. Mean and standard error of food types (%) in pygmy rabbits' (*Brachylagus idahoensis*) diets during summer and winter 2000, based on microhistological analysis of individual fecal samples from burrows at Sagebrush Flat, Washington, in areas grazed and ungrazed by cattle

Season	Grazing	*n*	Shrubs (%)		Grasses (%)		Forbs (%)	
			Mean	Standard error	Mean	Standard error	Mean	Standard error
Summer	Grazed	10	11.29	3.59	53.51	6.51	34.08	5.85
	Ungrazed	8	13.01	6.17	53.37	4.29	32.22	5.18
	Total	18	12.60*	3.29	53.45*	3.98	33.26*	3.88
Winter	Grazed	3	97.1	1.14	1.57	1.70	1.23	0.29
	Ungrazed	5	91.92	3.58	2.14	1.60	1.90	0.64
	Total	8	93.86*	2.37	1.92*	0.87	1.65*	0.41

Asterisk denotes significance between summer and winter for that food type at □=0.05. No significance was found for diets in areas grazed by cattle or ungrazed at □=0.05.

Before annual grazing in the spring, rabbits in ungrazed (p<0.05) and grazed areas (p<0.05) selected forbs over both grasses and shrubs, whereas grasses and shrubs were consumed in proportion to availability.

3.3. Composition and structure of vegetation

The overstory vegetation at SBF was dominated by big sagebrush with an understory grass cover dominated by *Poa sandbergii*, *Pseudoregneria spicata*, *Stipa comata*, *Bromus tectorum* and forb cover of *Astragalus* spp., *Plantago patagonica*, and *Draba verna* (for a more complete list see Appendix B, Siegel, 2002). Vegetation composition and structure differed little among grazing units in June before annual grazing began at SBF. The only consistent difference between grazed and ungrazed units was that grazed units (1 and 2) had a higher density of mature sagebrush with little decadent material (age class 3) than did the ungrazed units (p=0.0252). Unit 2 (grazed) had a lower density of decadent sagebrush (age classes 5: p=0.0158 and 6: p=0.0097) than the other 3 units, and a higher canopy cover of native perennial forbs (p=0.0051) and grasses (p=0.0377) than the other grazed unit (1). The long-term ungrazed Unit 3, had less cover of Thurber's needlegrass (p=0.0011) and fleabane (*Erigeron* spp.) (p=0.0099). Age class distribution and height to first live material on sagebrush did not differ for any age class among

grazed and ungrazed units (p 0.05).

In general, sagebrush became taller and denser between 1996 and 2000 in all units. Canopy cover of medium shrubs increased (p<0.0001) between 1996 and 2000, which was reflected in the increase of sagebrush cover from 12.1% to 16.9% (p<0.0001) and gray rabbitbrush (*Chrysothamnus nauseosus*) from 0.30% to 0.83% (p=0.0270). Sagebrush density increased from 9386 to 11,486 plants/ha (p=0.0007) between 1996 (0.44 m) and 2000 (0.51 m), and average sagebrush height increased for all age classes (p<0.0001) except for class 2. Total vegetative cover, however, decreased across SBF from 1996 (90.9%) to 2000 (72.5%, p<0.0001), with a decrease in forbs and grasses, including Sandberg's bluegrass (p<0.0001).

The amount of bluebunch wheatgrass consumed by cattle between 1997 and 2000 on Units 1 and 2 were 0.46 AUMS/ha and the combined use of bluebunch wheatgrass and Thurber's needlegrass was 50.6% in Unit 1 and 60.7% in Unit 2 (Table 2).

Table 2. Use in animal unit months (AUMs), or the amount of forage needed to feed one cow for one month, of grazing units by cattle at Sagebrush Flat, Washington, from 1996 to 2000 in grazed units: 1 (grazed during the dormant season for grass growth from 16 June to 29 February), 1A (grazed in 1996 and thereafter excluded from grazing), and 2 (grazed according to ecosystem standards set by the State of Washington legislature)

Year	Unit	AUM	AUM (ha)	Dates in	Dates out	Bluebunch wheatgrass used (%)
1996	Units 1 and 1A	101	0.18	19-Jul	4-Sep	–
	Unit 2	180	0.40	11-Nov	5-Dec	–
1997	Unit 1	77	0.21	4-Aug	23-Aug	17.4
	Unit 2	0				0
1998	Unit 1	238	0.65	22-Jun	10-Jul	56.3
	Unit 2	190	0.42	5-Feb	25-Feb	16.5
		275	0.61	28-Sep	27-Nov	58.2
1999	Unit 1	101	0.28	8-Sep	30-Oct	54.9
	Unit 2	215	0.47	3-Nov	15-Dec	38.0
2000	Unit 1	252	0.69	1-May	12-May	44.6
				13-Oct	25-Nov	
	Unit 2	49	0.11	15-Apr	1-May	37.9
		105	0.23	15-Jul	31-Jul	49.7
				25-Nov	30-Nov	
Total 1997–2000	Unit 1	668	1.83	–	–	–
	Unit 2	834	1.84	–	–	–
Mean 1997–2000	Unit 1	167	0.46	–	–	43.3
	Unit 2	209	0.46	–	–	50.1

3.4. Nutritional quality of pygmy rabbit forages

The nutritional quality of grass and shrub forages differed seasonally. Cell wall content (NDF) of both grasses and shrubs was lower in summer than in winter and spring ($p<0.0005$, Table 3). Likewise, lignin and cutin (ADL) was lowest in the summer for shrubs ($p<0.0001$), but was lowest in winter for grasses (p 0.0001, Table 3). Protein was highest in the summer for both grasses and rabbitbrush and highest in the spring for all classes of big sagebrush (p 0.05, Table 3).

Table 3. Constituents of 4 forage types used by pygmy rabbits (*Brachylagus idahoensis*) at Sagebrush Flat, Washington during summer, winter, and spring of 2000–2001 from units grazed by cattle (G) and ungrazed units (U)

Species	Grazing		Dry Matter (%)	Fiber (%)	Lignin (%)	Protein (%)
Bluebunch wheatgrass (*Pseudoregneria spicata*)	Summer	G	93.80 A	67.18 B	4.68 A	5.40 A
		U	93.74	67.59	4.96	5.38
	Winter	G	93.01* B	77.57* A	4.09* B	2.35* B
		U	92.14	75.75	3.63	2.75
	Spring	G	92.71 B	77.59* A	5.62* A	2.54 B
		U	92.72	75.44	3.9	2.74
Needlegrass spp. (*Stipa* spp.)	Summer	G	93.77 A	70.04 B	4.77 A	6.25 A
		U	93.80	68.27	5.38	6.37
	Winter	G	93.15* B	76.45 A	3.62* B	2.76* B
		U	92.21	75.76	4.29	3.42
	Spring	G	92.82 B	77.28 A	5.13* AB	3.01 B
		U	92.97	75.59	4.29	3.49
Big sagebrush (*Artemisia tridentata*) (age classes 1–2)	Summer	G	89.29 A	39.62 B	10.89 B	9.54 A
		U	89.94	41.40	11.16	9.80
	Spring	G	89.21 A	47.47 A	15.20 A	11.22 B
		U	88.72	47.48	13.37	10.70
Big sagebrush (*Artemisia tridentata*) (age classes 3–5)	Summer	G	89.48 A	36.39 B	9.71* B	10.87 A
		U	89.85	38.45	11.3	10.47
	Winter	G	90.28* A	43.46 A	14.54* A	9.84 B
		U	87.43	43.08	12.83	9.99
	Spring	G	88.64 A	44.69 A	14.57 A	11.40 A
		U	87.65	40.43	12.32	11.22
Rabbitbrush spp. (*Chrysothamnus* spp.)	Summer	G	92.59 A	30.77 B	8.15* C	10.40 A
		U	92.55	33.26	9.59	10.41
	Winter	G	92.13* B	50.13 A	13.07 B	6.53 B
		U	90.73	50.73	13.09	6.26
	Spring	G	91.08 B	54.49 A	14.94 A	7.26 B
		U	91.61	56.68	14.76	6.38

Big sagebrush was collected from age classes 1 (seedlings not producing seeds), 2 (young plants that are not producing maximum seeds), 3 (mature plants with little to no decadent material), 4 (mature plants less than 25% decadent), and age class 5 (mature plants 25 - 50% decadent). Asterisk before values denotes a significant difference between grazed and ungrazed areas for that season (□=0.05) and different letters after values denote significant differences for each plant species among seasons (□=0.05).

In summer before cattle grazing began, forages were similar in nutritional quality among grazed and ungrazed areas, except mature sagebrush and rabbitbrush, which had more lignin and cutin (ADL) in ungrazed than grazed units ($p<0.02$, Table 3). However, in winter and spring, after late summer and fall grazing but before green-up, both grasses had more fiber (either NDF or ADL or both, $p<0.04$), and in winter both grasses had less protein ($p<0.05$, Table 3). In winter, mature sagebrush had more ADL in grazed than ungrazed units ($p=0.01$, Table 3). Immature sagebrush plants did not differ in nutritional constituents between grazed and ungrazed areas during any season ($p>0.05$, Table 3).

3.5. Other habitat features

Slopes at SBF were all <30% but were distributed differently between grazed and ungrazed areas of SBF ($\chi^2=24.74$, DF=4, $p<0.001$). Ungrazed areas had more area than expected between 0% and 5% slope ($p<0.05$) and less area than expected between 15% and 20% slope ($p<0.05$). However, based on burrow counts, slopes were used in proportion to availability by pygmy rabbits. The average percent slope at pygmy rabbit burrows across SBF was 3.4%. A majority (135 of 165) of the burrows were found on slopes <5% and all burrows were found on slopes <12.5%.

The average aspect at pygmy rabbit burrows was 214° across SBF and most burrows (63% of 165) were found on south and SW aspects. Aspects were not used in proportion to availability ($\chi^2=39.08$, DF=8, $p<0.001$). Southwest aspects ($p<0.05$) were used more than expected and SE aspects ($p<0.05$) were used less than expected. Thus, pygmy rabbits selected for SW aspects and against SE aspects to dig burrows. In general, SBF slopes to the south and aspects were distributed differently between grazed and ungrazed areas ($\chi^2=26.89$, DF=8, $p<0.001$). Ungrazed areas had less area of SE aspects than expected ($p<0.05$) but all other aspects were distributed equally between grazed and ungrazed areas.

Soil types were distributed differently between grazed and ungrazed areas ($\chi^2=63.80$, DF=5, $p<0.001$). There was more Zen-Horseflat complex soil type of 3–8% slope than expected in grazed areas ($p<0.05$) and less than expected in ungrazed areas ($p<0.05$). The largest proportion of burrows (21%) was found in Zen-Horseflat complex soil types of 3–8% slopes. Soil depths were also distributed differently between grazed and ungrazed areas ($\chi^2=64.42$, DF=4, $p<0.001$). Ungrazed areas had less area with soils between 50 and 100 cm ($p<0.05$), but more area with soils >150 cm ($p<0.05$). Discernible differences in use among soil depths, however, were not evident.

4. Discussion

The last remaining population of Columbia Basin pygmy rabbits residing at Sagebrush Flat in central Washington selected ungrazed areas, especially Unit 3 that was ungrazed by livestock since 1957, preferentially over grazed areas when constructing burrows. Burrow surveys conducted on the same random plots between 1995 and 2000, showed a steeper decline (67%) in numbers of active burrows in grazed units than on ungrazed

units (38%) (Musser and McCall, 2000). However, the reasons pygmy rabbits avoided grazed areas, especially in recent years, are not clear.

Habitat differed little among the grazing units. First, slope was uniformly low across SBF, but ungrazed areas contained significantly more SE aspects, avoided by pygmy rabbits, than grazed areas. Likewise, ungrazed areas contained significantly less of the soil type (Zen-Horseflat complex soils type of 3–8% slope) in which the largest proportion (21%) of pygmy rabbit burrows was found. Pygmy rabbits preferred soil depths >25 cm, which were evenly distributed across grazing units. Therefore, slope, aspect, and soils do not explain the distribution of pygmy rabbit burrows at SBF.

Similarly, in early summer before cattle grazing began at SBF, the composition, structure, and height of vegetation varied little among the grazing units. The only consistent difference was a greater cover of mature, but not decadent, sagebrush in grazed than in ungrazed units. In addition, plant cover at SBF in 1996 and 2000 was similar to that measured on historical Daubenmire plots located in undisturbed remnants of sagebrush steppe of Washington in 1988 (E. Bracken, WDFW, pers. comm.). Therefore, the timing and intensity of grazing at SBF has not modified the long-term composition and structure of the sagebrush community at SBF.

However, grazing during late summer and fall reduced the availability of grasses (and presumably forbs) by about 50% in the grazed units until the next growing season. Grasses provide nesting material and cover for pygmy rabbits and other wildlife species in sagebrush habitats (Oregon Zoo, 2001). In addition, grasses provided >50% and forbs >30% of the pygmy rabbit's diet in late summer, but <3% of the diet in winter at SBF (Table 1). Our analysis did not show that pygmy rabbits ate less grass in grazed areas or that pygmy rabbits selected different diets relative to availability between grazed and ungrazed areas before annual grazing, but after annual grazing rabbits may have had more difficulty obtaining grasses and forbs in grazed areas. Green and Flinders (1980) found that pygmy rabbits in southeastern Idaho selected grasses and forbs preferentially over shrubs, suggesting that forbs and grasses are an important component of their diet.

Not only did grazing reduce the biomass of grass available in grazed units, it also reduced the nutritional quality of grasses in winter and spring. Grasses had less protein and more fiber on grazed areas than ungrazed areas. Shrubs were also more fibrous in grazed areas in winter than in ungrazed areas. However, grasses, especially in the winter, had only half the crude protein and about 50% more fiber than sagebrush and rabbitbrush (Table 3), thus may not necessarily provide a superior nutritional source for pygmy rabbits. Although sagebrush is high in protein, it contains high levels of monoterpenes that inhibit the growth of rumen and cecal microorganisms (Nagy and Tangerdy, 1968; Schwartz et al., 1980). For herbivores, selecting a diet is often a tradeoff between toxicity and nutrients, and the mixed diet consumed by rabbits in ungrazed units may reflect attempts by rabbits to maximize energy and protein while limiting the effects of toxic secondary plant chemicals (Pfister, 1999; Freeland, 1991) found in sagebrush. Pygmy rabbits are one of the few animal species that can consume large amounts of sagebrush without noticeable toxicity. White et al. (1982) found that pygmy rabbits have developed

mechanisms to reduce the amount of monoterpenoids in stomach ingesta by 77% through the processes of mastication and ingestion. Captive pygmy rabbits at Washington State University (WSU, Pullman, WA) exhibited high levels of liver enzymes (Washington Animal Disease Diagnostic Lab, WSU, pers. comm.), suggesting detoxification and excretion of compounds found in sagebrush. Detoxification, however, requires energy and nutrients and may limit the lifespan of an animal (Illius and Jessop, 1995), thus grasses and forbs are likely critical to a pygmy rabbit's diet when available.

Besides the amount and quality of grass available, other differences among grazing units not related to habitat may have contributed to burrow distribution. First, during winter, cottontails used more pygmy rabbit burrows in grazed areas of SBF than in ungrazed areas. Cottontails, which do not dig their own burrows and often inhabit burrows dug by pygmy rabbits, may displace or compete with the smaller rabbit. However, at SBF, pygmy rabbits re-used burrows in the summer that had been occupied by cottontails the previous winter. Because 60% of the burrows cottontails used in the winter had not shown pygmy rabbit activity on the last date the burrow was checked, cottontails may have used burrows primarily after they were abandoned by pygmy rabbits. Second, cattle grazing may influence the use of habitat by pygmy rabbits in ways we did not measure in this study. For example, we and other field biologists have observed cattle collapsing pygmy rabbit burrows (L. Cooke, WDFW, pers. comm.; Rauscher, 1997). Additionally, the presence of cattle may attract predators like coyotes, compact soil, influence spread of disease, or directly disturb rabbits (Gahr, 1993; Ellison, 1960).

4.1. Management implications

Pygmy rabbits in the Northwest and the Great Basin did not co-evolve with large herds of ungulates. Large herbivores were limited to small populations of deer, wapiti (*Cervus canadensis*), and pronghorn (*Antilocapra americana*) until the early 1700s with the arrival of horses (Franklin and Dyrness, 1973). Cattle were not introduced to steppe vegetation of the Northwest until the mid-1800s (Daubenmire, 1988; Galbraith and Anderson, 1971). Neighboring populations of pygmy rabbits within the Great Basin existed at the time of peak livestock numbers (Rauscher, 1997; Katzner, 1994; Green, 1978; Williams, 1986) but it is unclear what effect grazing has had on those populations.

Fortunately, habitat at SBF does not seem to be permanently altered by livestock grazing that spanned nearly a century. However, grazing removes herbaceous vegetation during the dormant season, which lasts 8 months, thus reducing the quality and quantity available for food and cover for pygmy rabbits. The importance of herbaceous vegetation to the fitness of pygmy rabbits, a sagebrush specialist, can at this time only be speculated. However, coupling the Columbia Basin pygmy rabbit's preference for ungrazed areas at SBF and their endangered status, we suggest that cattle grazing may not be compatible with conservation efforts until future replications of grazing studies, and studies examining the nutritional value of native forages to pygmy rabbits, can be conducted. A conservative approach is not only important for managing the remaining Washington populations of pygmy rabbits, but also in selecting release sites for new populations.

Furthermore, sagebrush at SBF and likely elsewhere is becoming taller and denser and the cover of herbaceous vegetation is declining, most likely because of natural succession, fire suppression, recent weather events, and possibly cattle grazing. Habitat managers now face a critical dilemma of maintaining a sustainable suite of successional stages appropriate for pygmy rabbits and other sagebrush steppe inhabitants in few, small, protected areas that are highly vulnerable to loss by catastrophic events. On those remaining reserves, maintaining a healthy sagebrush steppe habitat is critical for the recovery of Columbia Basin pygmy rabbits, as well as other sagebrush steppe inhabitants that are currently threatened, endangered, or declining, including sage grouse, sharp-tailed grouse, sage thrasher (*Oreoscoptes montanus*), sage sparrow (*Amphispiza belli*), Washington ground squirrel, and white-tailed jackrabbits.

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