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Grazing in sagebrush rangelands in western North America: implications for habitat quality for a sagebrush specialist, the pygmy rabbit

Meghan J. Camp^{A,B,E}, Janet L. Rachlow^A, Lisa A. Shipley^B, Timothy R. Johnson^C and Kelly D. Bockting^D

^ADepartment of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844-1136, USA. ^BSchool of the Environment, Washington State University, Pullman, WA 99164, USA. ^CDepartment of Statistical Science, University of Idaho, Moscow, ID 83844-1136, USA. ^DWildlife Biologist, Bureau of Land Management, Dillon, MT 59725, USA.

^ECorresponding author. Email: meghan.camp@email.wsu.edu

Abstract. Livestock grazing is one of the primary uses of sagebrush rangelands in western North America; therefore, an understanding of the ecological implications of grazing on habitat quality for sagebrush-dependent wildlife is needed to help land managers balance multiple objectives for land use. We studied effects of cattle grazing on components of habitat for an uncommon sagebrush habitat specialist, the pygmy rabbit (Brachylagus idahoensis), which has been petitioned for endangered or threatened status in the USA. We evaluated multiple components of habitat before and after grazing in replicated control and treatment plots in a mesic, high-elevation sagebrush-steppe environment in south-western Montana, USA. We predicted that grazing would decrease the biomass of herbaceous forage, alter security cover, and increase rate of collapse of rabbit burrows, and we expected that these effects would be more pronounced during summer than spring. As expected, cattle grazing reduced the biomass of perennial grasses available to pygmy rabbits after grazing that occurred during either spring or summer, and the biomass of forbs after spring grazing. In contrast, grazing did not markedly influence the functional properties of vegetation related to predation risk or the integrity of rabbit burrow systems. In the context of the stocking rate of the allotments in our study (7.3 acres/Animal Unit Month, 2.95 ha/Animal Unit Month), annual cattle grazing did not seem to markedly change habitat for pygmy rabbits in our study area; however, longer-term and higher intensity grazing might result in more pronounced habitat changes. Understanding the ecological implications of cattle grazing on habitat quality for pygmy rabbits and other sagebrush-dependent wildlife can guide conservation strategies for these species on sagebrush rangelands managed under multiple-use policies.

Additional keywords: Artemisia, Brachylagus idahoensis, forage biomass, habitat specialist, sagebrush, security cover.

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Introduction

Balancing multiple land uses is a challenge that managers face on >1.8 million km² of public lands in the United States, primarily in the west of the country (Loomis 2002). A common challenge arises from the requirement to manage lands for two important, yet often conflicting objectives, i.e. fulfilling human needs for food, timber, energy, recreation, and other ecosystem goods and services, while also maintaining ecosystem functions and habitat for native wildlife species (Dale et al. 2000). Balancing human needs and ecosystem function is especially important for threatened wildlife species and ecosystems.

Sagebrush ecosystems cover large portions of 11 states in the Great Basin of the western United States and have a long history of multiple-use landscapes. However, as a result of

land-use changes during the past two centuries, sagebrush steppe is one of the most threatened ecosystems in the world (Anderson and Inouye 2001). Recent estimates indicate that sagebrush vegetation remains in only 46% of its original distribution in the Great Basin, and almost none of the remaining area is intact and unaltered (Miller et al. 2011). Over 350 species of plants and animals that inhabit these systems are considered to be species of conservation concern (Davies et al. 2011), including 11 mammals that are endemic to the shrub steppe in the inter-mountain west of the United States (Dobkin and Sauder 2004). In addition, these ecosystems support a diversity of sagebrush-dependent or obligate species (Dobkin and Sauder 2004). Such habitat specialists can be especially vulnerable to loss and alteration of habitat because a narrower range of environmental conditions can support their persistence compared with generalist species (Swihart *et al.* 2006).

Although diverse human activities influence sagebrush rangelands, e.g. recreation, oil and gas exploration and extraction, and urban expansion, livestock grazing is currently one of the most extensive uses, as it has been over the past century (Sanderson 2002; Davies et al. 2011). Grazing by domestic livestock can alter the composition, diversity and phenology of plant communities (Loft et al. 1987; Augustine and McNaughton 1998; Diaz et al. 2007; Veblen and Young 2010). Grazing also can affect soil properties through compaction, erosion and changes in plant communities and water quality through faeces and urine deposition (Sanderson 2002). Because sagebrush ecosystems in the western United States did not evolve with domestic cattle (Franklin and Dyrness 1973), maintaining sagebrush habitats that are also suitable for native mammals under cattle grazing regimes requires an understanding of how grazing alters habitat functions for sagebrush-dependent species.

The pygmy rabbit (Brachvlagus idahoensis) is a sagebrushdependent mammal that occurs in sagebrush habitats in the Great Basin and the surrounding inter-mountain region of the United States. This species is one of only three vertebrates that feed primarily on sagebrush, which is chemically defended against herbivory (Shipley et al. 2012). During winter, the diet of pygmy rabbits consists almost entirely of sagebrush, and during spring and summer, their diet comprises ~50% sagebrush and 50% grasses and forbs (Green and Flinders 1980; Siegel Thines et al. 2004). In addition, big sagebrush (Artemisia tridentata vaseyana) provides their primary source of security cover from a diverse suite of avian and terrestrial predators (Green and Flinders 1980; Price et al. 2010; Camp et al. 2012). Sagebrush ecosystems, used for livestock grazing, overlap considerably with areas occupied by pygmy rabbits. Potential effects of this land use on habitat features that influence survival and reproduction for pygmy rabbits are poorly understood, although frequently postulated (Rauscher 1997; United States Fish and Wildlife Service 2003; Siegel Thines et al. 2004). Understanding potential effects is important for managers of both public and private lands because the pygmy rabbit is considered a species of conservation concern throughout its range. A distinct population in Washington State is federally listed as endangered under the US Endangered Species Act, and the entire species was previously petitioned for federal threatened or endangered status (United States Fish and Wildlife Service 2003, 2010).

Grazing by cattle has the potential to alter habitat indirectly for pygmy rabbits in at least three ways. First, cattle grazing can reduce the amount of forage for pygmy rabbits during summer when their diet includes both grasses and forbs (Green and Flinders 1980; Siegel Thines *et al.* 2004). Because cattle feed predominately on herbaceous plants, they can reduce the forage mass of grasses and forbs through direct consumption over short time periods or by changing the plant composition of the community over longer time periods (Ellison 1960; Huntly 1991; Fleischner 1994; Knick 1999). Second, grazing, that removes the herbaceous understory, also might reduce security cover for pygmy rabbits. Third, removal of grass and forb forage can reduce competition for water and soil nutrients, resulting in an increase in the height and density of sagebrush shrubs (Laycock 1991; Siegel Thines *et al.* 2004). An increase in sagebrush could enhance concealment cover from predators, thermal protection and winter food availability for pygmy rabbits. In addition, because pygmy rabbits are obligate burrowers, cattle could influence their habitat directly by physically collapsing burrow entrances (Rauscher 1997; Siegel Thines *et al.* 2004). Although collapsed burrows of pygmy rabbits have been documented when cattle were present (Rauscher 1997), no empirical evidence is available as to whether cattle increase rates of burrow degradation.

The aim of this study was to quantify how cattle grazing during two seasons (spring and summer) in a mesic, highelevation sagebrush-steppe ecosystem might alter multiple habitat components for pygmy rabbits. We predicted that cattle grazing would (1) decrease the mass of herbaceous forage, (2) alter security cover, specifically the functional properties of concealment and visibility (Camp et al. 2013), and (3) increase the rate of collapse of burrows. We expected that these effects would be more pronounced during summer than spring due to greater rainfall and plant growth during the spring. We established replicated pairs of grazed and control plots and quantified forage mass and the functional properties of cover within the plots, and we evaluated the integrity of burrow systems before and after grazing treatments. Because cattle grazing is a pervasive use of the sagebrush ecosystem, a better understanding of how grazing does or does not affect habitat quality for this sagebrushdependent mammal can inform decisions about how to balance this land use with conservation objectives.

Material and methods

Study area

We conducted a field manipulation of cattle grazing and measured components of pygmy rabbit habitat in south-western Montana, during the spring and summer of 2011. The study area had a continental climate with cold, dry winters and dry summers; average annual precipitation was 250 mm, and most of the precipitation occurred during May and June (Western US Climate Historical Summaries 2011). The vegetation was dominated by mountain big sagebrush with a relatively open and patchy shrub canopy (cover, $21.3 \pm 2.7\%$) and an understory of native grasses and forbs.

The field experiments were conducted within the Reservoir Creek area (RC, Fig. 1). The study area was divided into eight large pastures ranging in size from 600 to >1500 ha that were on a rest-rotation grazing schedule (Table 1). Six of the pastures were grazed sequentially for ~5 weeks starting in May until August; those that were grazed from May until June were considered the spring-grazing treatments, and the ones that were grazed between June and August were considered the summer treatments. The average stocking density over the 5 weeks was 10.37 Animal Units (AU) ha-1, where 1 AU was 1000 lbs of grazing animal, and the utilisation was <45% (R. Martin, pers. comm.). For comparison, $16.8 \text{ AU} \text{ ha}^{-1}$ is the highest recommended level for this type of site in good condition in Montana (clavey/silty, deep soils with 250-350 mm annual precipitation; Lacey and Taylor 2005), and average stocking density across all allotments managed by the Bureau of Land Management in this region was 11.11 AU ha^{-1} .



Fig. 1. Location of the study area in south-western Montana, USA, (inset) with the Reservoir Creek site (8281 ha) showing the arrangement of the pastures and paired treatment plots where effects of cattle grazing on habitat for pygmy rabbits were studied. Each plot pair consisted of a plot excluded from grazing during the current grazing season and a plot open to grazing.

 Table 1.
 The grazing schedule for the Reservoir Creek study site in south-western Montana in 2011 and the dates when forage mass, shrub cover, concealment and visibility were measured

A total of 375 cattle were rotated through Cross, W-2 and R-4 pastures, and 250 cattle were rotated through R-1W, R3 and R-1E pastures

Pasture	Area (ha)	Grazing season	Grazing dates (2011)	Measurement dates (2011)		
R-4	1078	Spring	16 May-18 June	22 June–24 June		
R-1E	661	Spring	16 May–18 June	19 June–21 June		
R-1W	1286	Summer	14 June–12 July	13 July-22 July		
Cross	1507	Summer	19 June–22 July	23 July–25 July		
R-3	903	Summer	13 July-10 August	10 August-13 August		
W-2	1199	Summer	23 July-25 August	26 August		
R-2	605	Not grazed	Not grazed	Not measured		
W-1	1046	Not grazed	Not grazed	Not measured		

One of the pastures (R1-W) contained two long-term grazing exclosures (0.4 ha each) that had not been grazed by cattle since 2001. Habitat measurements were collected within these two long-term grazing exclosures, which provided an opportunity

to compare habitat that was currently grazed with habitat in which grazing had been excluded for 10 years. Because there were only two long-term exclosures, the results were interpreted qualitatively.

To estimate the effects of cattle grazing on forage mass, data were collected after spring and summer grazing in 36 plots within six of the large pastures (Table 1). In each pasture, three 12×12 -m grazing exclosures, made of electrified poly wire, were set up and a paired plot of the same size next to each exclosure that was open to cattle grazing was identified. Therefore, each pair of plots had two treatments, grazed and ungrazed in the current year. The locations of the plots were randomly generated in a GIS and located >1 km apart and $>100 \,\mathrm{m}$ from a road, at elevations ranging from 1617 m to 2096 m, and at slopes between 2 and 20%. The fences for both the annual and long-term exclosures were ~1.2 m high to exclude cattle but native ungulates and other browsing species could potentially enter the exclosures. The pasture that contained the long-term exclosures was only grazed during the summer; therefore, the long-term exclosures were sampled only during the summer season.

Vegetation structure and forage mass

Each pasture was sampled immediately following cattle grazing (Table 1). Forage mass was sampled by clipping and separating by genus all live (i.e. new growth) forage mass in 12 (0.5×0.5 -m) microplots that were systematically distributed within each of the 12 × 12-m sample plots. A total of 38 sample plots (18 grazed, 18 ungrazed, two ungrazed long-term exclosures) and 456 microplots was sampled. Samples were dried at 100°C for 24 h before weighing.

Two functional properties of security cover for prey species are concealment and visibility (Camp et al. 2013), and the effects of grazing on both of these functional properties were evaluated. Both concealment and visibility were estimated at 10 systematically distributed points per sample plot. At each point, concealment (i.e. the extent to which vegetation would hide pygmy rabbits from potential terrestrial predators) was measured using a standard technique (Griffith and Youtie 1988) modified in size for our species. A profile board of the approximate size of a pygmy rabbit $(15 \times 15 \text{ cm with } 25 \text{ } 3 \times 3 \text{ cm red and white})$ squares) was viewed from a horizontal distance of 4 m at an eyeheight of 1 m. Similarly, to measure concealment from aerial predators, the profile board was placed flat on the ground and a perpendicular photograph taken from a height of 1.5 m. From both terrestrial and aerial perspectives, the number of 3×3 -cm squares that were \geq 50% obstructed by vegetation were recorded.

To measure visibility of potential predators from the perspective of the pygmy rabbit, a camera on a tripod at a height of 8 cm was used to represent the approximate eye level of a pygmy rabbit (Camp *et al.* 2013). A 1×1 -m board placed at 4 m from the camera was photographed. The proportion of the 1×1 -m board that was visible to the pygmy rabbit was estimated by placing a digital grid with 100-point intersections over the digital photograph on a computer and recording the number of intersections at which the board was visible (i.e. not obscured by vegetation). This count provided an index of visibility of terrestrial predators from the pygmy rabbit's perspective. To assess visibility of aerial predators, a photograph was taken directly upward from each point and the number of grid intersections in which the sky was visible in the photograph was recorded.

Burrow integrity

To evaluate the effects of grazing on the integrity of burrows of the pygmy rabbit, active burrow systems were mapped, and the activity status of all entrances of burrows for each burrow system before grazing was counted and rated. Burrows of the pygmy rabbit were identified as active based on the presence of fresh pellets according to an established survey protocol for this species (Sanchez *et al.* 2009; Price and Rachlow 2011). After grazing, the burrows were revisited to compare the activity status with that of the pre-grazing condition. At each burrow system, the presence or absence of cattle hoof prints and dung within 3 m of any burrow entrance was also recorded. Data on 89 active burrow systems (238 burrow entrances) throughout the RC area were collected.

Data analyses

The total forage mass, forage mass of functional groups (grasses, shrubs and forbs), individual plant genera, concealment and visibility between grazed and ungrazed treatments and between seasons (spring: mid May-mid June; and summer: mid June-late August) were compared using mixed-effects linear models (PROC MIXED, SAS 9.2, SAS 2008). The fixed effects of season and treatment and their interaction were included. Random effects were specified for the effects of pasture and for sample plots nested within pastures. The variance for the random effect of pasture was estimated as zero, so this effect was dropped from the model. Significant results were followed with pair-wise comparisons. Excluding the long-term exclosures, six pastures with three pairs of sample plots (grazed and ungrazed) we sampled and, therefore, the sample size was 36 total sample plots. Each pasture was >600 ha (Table 1) and each pair of plots was >1 km apart to ensure independence among the three pairs of plots per pasture. The long-term exclosures were only grazed and sampled during the summer season, and separate analyses were conducted for all measures using the same models but a third treatment of long-term ungrazed was included in the models.

To compare the integrity of the entrances of the burrows after cattle grazing with the pre-grazing condition, a generalised linear mixed-effects model with a binomial distribution was used (PROC MIXED, SAS 9.2, SAS 2008). The response variable was the proportion of collapsed entrances of burrows at each burrow system. The fixed effects were grazing (pre- or post-), pasture and their interaction. Because the entrances of the burrows were part of distinct burrow systems, we included the random effect of burrow system. If cattle were not influencing the integrity of burrow systems, it was expected that, after short periods of grazing, such as 4–5 weeks, the proportion of collapsed to open entrances of burrow would not differ. This work was approved by the University of Idaho IACUC (Protocol 2010–19), although no live animals were used in this portion of the research.

Results

Forage mass

As expected, grazing by cattle reduced the total forage mass at the study sites (Fig. 2). There was a reduction in the forage mass of perennial grasses in grazed plots compared with ungrazed plots (Fig. 2). Perennial grasses present at the sites included grasses from the genera *Agropyron*, *Elymus*, *Festuca*, *Hordeum*, *Hesperostipa, Poa* and *Pseudorogeneria*, which have, with the exception of *Hordeum*, been documented in the diets of pygmy rabbits (Green and Flinders 1980; Gahr 1993; Siegel Thines *et al.* 2004; Woods 2012). The forage mass of perennial grasses was significantly influenced by season, treatment, and the interaction between season and treatment (Table 2). Differences in least-squares means demonstrated that grazing during both seasons reduced the forage mass of perennial grasses (spring, t=5.95, P < 0.01; summer, t=3.39, P < 0.01).

Forage mass of perennial forbs was influenced by season and treatment, but not by their interaction (Table 2). Differences in least square means indicated that the forage mass of perennial forbs was higher in the spring than the summer (t=3.97, P<0.01) and on ungrazed plots compared with grazed plots (t=2.53, P<0.05). The dominant genera of perennial forbs present at the sites included *Lupinus*, *Phlox*, *Astragalus*, *Aster*, *Arnica* and *Antennaria*. Most (except *Aster* and *Arnica*) have been documented in the diets of pygmy rabbits (Green and Flinders 1980; Gahr 1993; Siegel Thines *et al.* 2004; Woods 2012). Grazing did not appear to significantly influence the forage mass of sagebrush. Annual forbs and grasses were extremely rare at the study sites (<0.004% of the total forage mass) and were not included in the analysis.

Only the forage mass of some genera were significantly influenced by grazing during spring and summer. Of the 47 genera, 12 genera comprised $\geq 1\%$ of the total forage mass that in grazed and ungrazed plots. Of those 12 genera, the forage mass from the genera *Antennaria*, *Festuca*, *Poa* and *Pseudorogeneria* were significantly reduced by cattle grazing when both seasons

were combined (P < 0.05). Antennaria, Festuca, and Poa species were reduced after spring grazing and Agropyron and Hesperostipa species were reduced after summer grazing (Table 3).

Security cover

Contrary to our expectations, cattle grazing during the current year in did not markedly alter either of the functional properties of security cover, concealment (the ability of vegetation to hide pygmy rabbits) and visibility (the potential for pygmy rabbits to observe approaching predators). Concealment from terrestrial predators in the experimental plots did not differ significantly by either season or grazing treatment (grazed, $\bar{X} = 44\%$, s.e. = 2.7%; ungrazed, $\bar{X} = 46\%$, s.e. = 2.7%; P > 0.10). Likewise, visibility of potential terrestrial predators from the perspective of pygmy rabbits did not differ between seasons or treatments (grazed, $\overline{X} = 56\%$, s.e. = 2.4%; ungrazed, $\overline{X} = 53\%$, s.e. = 2.4%; P > 0.10). Similarly, concealment from aerial predators (grazed, $\overline{X} = 6.4\%$, s.e. = 1.3%; ungrazed, $\overline{X} = 6.7\%$, s.e. = 1.29%) and visibility of aerial predators (grazed, $\overline{X} = 96\%$, s.e. = 0.96%; ungrazed, \bar{X} = 96.2%, s.e. = 0.93%) also were not markedly affected by either season or grazing treatments (P > 0.50).

Burrow integrity

Contrary to our expectation, spring and summer cattle grazing during a 5-week period did not influence the integrity of entrances of pygmy rabbit burrows, even though most of the burrow



Fig. 2. Forage mass (mean \pm s.e.m.) of plant functional groups in grazed and ungrazed plots during (*a*) spring and (*b*) summer of 2011 at the Reservoir Creek site in south-western Montana, USA. Significant differences (P<0.05) are denoted with an asterisk (*) above the bars. For consistency, the effects of spring and summer are shown separately, although the interaction between season and treatment was not significant for perennial forbs.

Table 2. Degrees of freedom (d.f.) and *F*- and *P*-values from the mixed-model analysis, testing the fixed effects of season (as a class variable), treatment (as a class variable) and their interaction for perennial grasses and perennial forbs sampled in the Reservoir Creek area in Montana, USA, 2011

	Season (spring and summer)		Treatment (grazed and ungrazed)			Season × treatment			
Trait	d.f.	F	Р	d.f.	F	Р	d.f.	F	Р
Total forage mass	1,18	13.3	< 0.01	1,18	21.5	< 0.01	1,18	8.71	< 0.01
Perennial grasses	1,16	10.3	< 0.01	1,16	46.42	< 0.01	1,16	8.43	0.01
Perennial forbs	1,16	15.74	< 0.01	1,16	6.41	0.02	1,16	2.37	0.14
Sagebrush	1,16	4.75	0.04	1,16	0.13	0.72	1,16	2.41	0.14

Table 3.	Forage mass (mean ± s.e.m.) of plant genera sampled in grazed and ungrazed plots during spring (mid May-mid
Jui	ne) and summer (mid June–late August) of 2011 at the Reservoir Creek area in south-western Montana

Significant differences (P < 0.05) based on differences in least square means from a mixed-effects linear model are denoted with an asterisk (*). For consistency, pair-wise comparisons were separated by season, although, in some cases, the interaction between treatment and season was not significant. Degrees of freedom (d.f.) and *t*-values are also given

Season	Genus	Forage mass (kg DM ha^{-1})				t	Р
		Grazed	Ungrazed	s.e.m.	d.f.		
Spring	Agropyron	0	0	0	_	_	_
	Antennaria	14	39.2*	12.8	16	-2.35	0.03
	Artemisia	95.2	122	25.2	16	-1.17	0.26
	Aster	9.6	18	6	16	0.36	0.72
	Astragalas	46.4	46	14	16	0.05	0.96
	Ericameria	1.2	4	3.2	16	-0.96	0.35
	Festuca	108	136*	39.6	16	-2.15	0.05
	Hesperostipa	0	0	0	_	-	_
	Lupinus	3.2	21.6	8.8	16	-1.77	0.09
	Phlox	33.2	29.2	9.6	16	0.41	0.68
	Poa	57.2	111.2*	12	16	3.43	0.0005
	Pseudorogeneria	22.8	43.2	25.6	16	-1.59	0.13
Summer	Agropyron	22	38.8*	11.6	16	-2.41	0.03
	Antennaria	12	22.4	9.2	16	-1.37	0.19
	Artemisia	56.8	40	18	16	1.03	0.32
	Aster	6.8	8.4	4.4	16	-0.36	0.72
	Astragalas	4.8	10.8	10	16	-0.72	0.48
	Ericameria	6	4	2.4	16	0.98	0.34
	Festuca	24	32	28	16	-0.49	0.63
	Hesperostipa	6.4	11.2*	4.4	16	-2.21	0.04
	Lupinus	0.4	1.2	6	16	-0.17	0.88
	Phlox	16	20	6.8	16	-0.59	0.56
	Poa	6.4	6.4	8.8	16	-0.03	0.98
	Pseudorogeneria	28	84	18	16	-1.87	0.08

systems had hoof prints, indicating that cattle were using areas immediately around them. Although the proportion of collapsed entrances of burrows was slightly higher after grazing (pregrazing, 20% collapsed, 38/196; post-grazing, 27% collapsed, 53/196), the difference was not significant ($F_{1,86}$ =2.46, P=0.12). Likewise, neither pasture ($F_{2,86}$ =0.89, P=0.41) nor the interaction between the grazing and pasture ($F_{2,86}$ =0.39, P=0.67) was significant. However, 75 out of 89 burrow systems (84%) had cattle hoof prints and 47 (53%) had dung <3 m from a burrow entrance after grazing, indicating that cattle had been present on or around the burrow systems. Nevertheless, grazing for 4–5 weeks at a mean stocking density of 10.37 AU ha⁻¹ did not markedly alter the integrity of burrow systems for pygmy rabbits.

Long-term effects

After a decade of cattle exclusion, plots within the long-term exclosures tended to have greater forage mass for pygmy rabbits. Estimates of total forage mass, as well as perennial grasses and forbs, were higher, although not significantly, in the long-term exclosures than in the plots excluded from grazing during only the current year (Fig. 3). In contrast, shrub mass did not exhibit a similar trend (Fig. 3). Contrary to expectations, functional components of security cover were similar between the grazed plots and those with long-term exclusion of cattle (concealment: grazed, \bar{X} = 39.5%, s.e. = 3.33%; ungrazed, \bar{X} = 44.86%, s.e. = 3.16%; long-term exclosure, \bar{X} = 61.4%,



Fig. 3. Forage mass (mean \pm s.e.m.) of plant functional groups sampled in plots that were grazed in the current year (grazed), ungrazed for 1 year (ungrazed), and ungrazed for 10 years (LT ungrazed) during summer 2011 at the Reservoir Creek site in south-western Montana, USA.

s.e.=7.12%; visibility: grazed, \bar{X} =63.1%, s.e.=2.95%; ungrazed, \bar{X} =56.83%, s.e.=2.94%; long-term exclosure, \bar{X} =43.3%, s.e.=7.22%; P > 0.10), suggesting that security cover available to rabbits was not significantly altered by grazing at this site, even after 10 years of release from grazing.

Discussion

Cattle reduced availability of forage for pygmy rabbits, including the forage mass of perennial grasses after grazing during both spring and summer grazing, and forage mass of perennial forbs. Although grazing reduced the abundance of some forage genera that are components of the diet of pygmy rabbits, presence of cattle did not markedly influence properties of vegetation related to predation risk or integrity of burrow systems at the stocking rates in this study.

Grazing by cattle across both spring and summer reduced the availability of perennial grasses and forbs. This result was expected and is consistent with studies that have documented that grazing by domestic livestock reduced the abundance of forage available to other wildlife, such as mule deer (Odocoileus hemionus; Austin et al. 1983; Bowyer and Bleich 1984) and elk (Cervus elapus; Skovlin et al. 1983). Diets of cattle in sagebrush systems typically consist of 280% grasses during spring (Ngugi et al. 1992; Beck and Peek 2005). Use of Festuca and Poa species by cattle in this study reduced availability of these important forage species for pygmy rabbits, most notably after spring grazing. Based on analysis of fecal pellets, these genera were commonly consumed by pygmy rabbits at our study sites (8% of the diet comprised Festuca species and 9% comprised Poa species; Woods 2012). Although some research has demonstrated that carefully managed grazing during the spring can increase the digestible protein and energy content in grass species (Clark et al. 2000; Brewer et al. 2007), the nutritional value of forage (i.e. digestible protein) to herbivores was not significantly influenced by cattle grazing at our study site during either spring or summer (Camp 2012). A reduction in the forage mass of grasses of 25-50% was found during the seasons when pygmy rabbits are reproducing and, although forage mass of grasses might not have limited the population, this reduction might require pygmy rabbits to forage over larger areas or to spend more time foraging, which could increase exposure to predation risk. Addressing these issues would facilitate an evaluation of the biological significance of the documented change in forage availability for pygmy rabbits as a result of cattle grazing.

The lack of a significant effect of grazing on functional components of security cover suggested that the foraging and other activities of cattle did not markedly alter the structure of vegetation to the extent of increasing vulnerability of pygmy rabbits to predators in this study. Other research has documented that grazing can reduce security cover for wildlife (Loft et al. 1987; Bock et al. 1993), and livestock grazing has been implicated as a potential factor associated with widespread declines of greater sage-grouse (Centrocercus urophasianus) because of a decrease in security cover (Connelly and Braun 1997). Brown hares (Lepus europaeus) in a Mediterranean rangeland in central Macedonia, Greece, used moderately grazed habitats more intensively than ungrazed and lightly grazed habitats (Karmiris and Nastis 2007). The authors concluded that the reduction in forage abundance was not a driving force for pasture selection, but the hares might prefer the moderately grazed pastures because they are more likely to visually detect predators while feeding in areas with a limited herbaceous layer (Karmiris and Nastis 2007). Similarly, jackrabbits (Lepus spp.) in southern Arizona showed a preference for areas where livestock

grazing had reduced herbaceous cover, but there was still moderate forage supply available (Taylor et al. 1935). In contrast, other researchers have suggested that grazing might increase the cover of shrubs in sagebrush habitats, which could provide more security cover for pygmy rabbits (Siegel Thines et al. 2004). Camp et al. (2013) focussed on the mechanistic link between vegetation and security rather than on vegetation cover per se, and did not detect differences between grazed and ungrazed treatments in the functional components of security cover as they pertain to a small mammal, even when plots were examined from which grazing had been excluded for 10 years. Camp et al. (2012) previously demonstrated that pygmy rabbits respond to these functional components of security to reduce predation risk at fine spatial scales (and, although mean values did not differ between grazed and ungrazed plots, it is possible that the variability or distribution of security cover might have been altered but undetected.

The annual grazing treatments did not markedly influence the integrity of burrows created and used by pygmy rabbits. Based on the presence of dung and hoof prints, cattle were present at the majority of the burrow systems, and yet their presence did not significantly influence the integrity of the entrances relative to the pre-grazing condition. If effects of cattle presence are cumulative over time, however, the duration of annual grazing in the treatments (5 weeks) might not have been long enough to cause a detectable effect on burrow systems given their sample size (n = 196 burrows). In addition, pygmy rabbits are prolific diggers (Sanchez et al. 2009) and, therefore, even if a greater number of entrances were collapsed by cattle, it is possible that the openings were re-excavated before the burrow system was evaluated immediately following grazing. Other studies have documented cattle damaging burrows of desert tortoises (Gopherus agassizii; Avery and Neibergs 1997) and trampling soil so that it was no longer suitable for burrow construction by small mammals (Torre et al. 2007). However, another burrowing mammal, the Utah prairie dog (Cynomys parvidens), showed an increase in density of active burrows within grazed pastures over 3 years (Elmore and Messmer 2006). In this study, cattle grazing did not directly influence the habitat of pygmy rabbits in terms of altering the integrity of burrow systems.

The average stocking rate for the RC grazing allotments was 10.37 AU ha^{-1} . Additionally, these allotments are on a restrotation system, which provides a period of rest or deferment during the growing season for grasses that are selectively grazed by cattle and helps to maintain plant communities (Briske *et al.* 2008). No invasive species were found, which also suggests that the current stocking rates and grazing systems have not negatively influenced the composition of the vegetation communities.

The results suggest that the current stocking rate has limited effects on habitat for pygmy rabbits and is an appropriate level for this species in this area. Although several studies have examined the effects of cattle grazing on wildlife, relatively few studies have focussed on the effects of grazing on lagomorphs. A handful of studies on the effects of grazing on rabbits in other ecosystem types, such as Mediterranean rangelands and short-grass prairies, suggest that lagomorphs and cattle may be compatible when stocking rates do not exceed cattle-grazing

capacity (Taylor *et al.* 1935; Karmiris and Nastis 2007; Wallis De Vries *et al.* 2007).

Other factors, such as soil properties, vegetation composition, and seasonal weather, and not examined in this study, also might influence how cattle could alter habitats for wildlife. Although a split plot design for the sampling protocol was used to match potential abiotic and biotic factors when comparing grazed and ungrazed treatments, the treatments were only imposed during a single year, which removes annual variation in weather as a potential confounding effect, but does not allow us to address how plants might respond to grazing differently across years. Future work is needed to address how variation in factors, such as soil type, vegetation composition or annual weather, might influence how cattle grazing affects the habitat of pygmy rabbits. Such work is needed in other areas of the sagebrush-steppe to provide spatial and temporal context for understanding how land managers might balance grazing by livestock with the habitat needs for sagebrush-dependent mammals like pygmy rabbits.

The data that was collected within two areas from which cattle grazing had been excluded for 10 years, suggested that long-term grazing by cattle had a cumulative influence on forage availability for pygmy rabbits, but not on the components of vegetation structure related to their vulnerability to predation. However, a more complete understanding of this system will require a more extensive temporal perspective. These plant communities, which have experienced grazing by livestock for >150 years might be in an ecologically stable (i.e. nontransitory) state; therefore, 10 years of cattle exclusion might not be sufficient time to move succession to a different state (Yeo 2005). In addition, other native herbivores, including elk, deer, and pronghorn, were present also in the study area and potentially grazed within the long-term enclosures. Exclusion of grazing by both wild and domestic ungulates for long periods of time (>40 years) has been shown to increase shrub cover and decrease diversity of sagebrush plant communities, and the effects of grazing of wild ungulates seems to be intermediate to the combined effect of livestock and wild herbivores (Manier and Hobbs 2007). Long-term studies are challenging to implement but critical for understanding the influence of multiple land uses over timeframes that are ecologically meaningful.

If pygmy rabbits are not limited by the abundance of herbaceous forage, then these results suggest that the indirect and direct effects of annual seasonal grazing as conducted during this study might be compatible with persistence of pygmy rabbits in this habitat. Measurements within the long-term grazing exclosures, however, suggested that the cumulative effects of grazing on forage availability might be more pronounced and, consequently, deserve greater attention. A better understanding of the influence of cattle grazing on habitat quality for sagebrush wildlife can help managers balance the inherent trade-offs between fulfilling human needs and maintaining biodiversity in sagebrush-steppe rangelands.

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