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Livestock Use Has Mixed Effects on Slender Orcutt Grass in Northeastern California Vernal Pools☆,☆☆,★

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ABSTRACT

Land managers often face the dilemma of balancing livestock use with conservation of sensitive species and ecosystems. For example, most of the remaining vernal pools in California are grazed by livestock. Vernal pools are seasonal wetlands that support many rare and endemic species, such as slender Orcutt grass (*Orcuttia tenuis* Hitchc.). Although studies in other areas of California have demonstrated that livestock use may benefit some vernal pool specialist species, grazing has been considered a threat to slender Orcutt grass in northeastern California. We evaluated the effects of livestock use on slender Orcutt grass using a replicated, paired design across a range of environmental conditions and grazing management regimes. Frequency, density, cover, reproductive potential, and height of slender Orcutt grass was compared in plots where livestock had been excluded with plots where grazing occurred. We found that livestock do not directly graze slender Orcutt grass, so the effects of livestock use on this species are indirect. These indirect effects are complex, including both positive, neutral, and negative effects. Year had the largest effect on slender Orcutt grass, probably as a result of variation in annual precipitation patterns. Livestock use had no effect in some years; in other years slender Orcutt grass was twice as abundant in unfenced than in fenced plots. Litter cover was also lower in unfenced plots in these years, suggesting that livestock use may benefit slender Orcutt grass in some years by reducing litter accumulation. Conversely, livestock use negatively affected slender Orcutt grass in pastures where livestock hoofprint cover was high, including pastures that were grazed early in the season. By considering patterns of annual variation in environmental factors such as precipitation, site conditions, and season of grazing, land managers can balance the needs of sensitive vernal pool species with maintaining livestock utilization on public lands.

1. Introduction

Livestock grazing is one of the primary uses of public lands across the western United States. Federal agencies, including the Bureau of Land Management (BLM) and the Forest Service, manage livestock use on 251 million acres, producing nearly 15 million animal unit months of forage per year (USDA 2014; USDI 2014). Public lands also support many rare species and habitats, and livestock use is commonly observed to be detrimental to biodiversity (e.g., Fleischner 1994; Evans et al. 2015). However, in certain ecosystem types, particularly those where species have evolved with grazing pressure, grazing can help to maintain diversity and complete removal of ungulate herbivory can have adverse impacts (Collins et al. 1998; Fuhlendorf and Engle 2001; Weiss and Jeltsch 2015). Effects of livestock use on particular species of conservation concern can be difficult to predict because the strongest effects of large herbivores are often indirect and related to various ecological processes including nutrient cycling, fuels and fire regimes, plant-plant interactions, trophic dynamics, and habitat modifications (Hobbs 1996; Weisberg and Bugmann 2003; Veblen and Young 2010). Land managers often face the dilemma of balancing livestock use with the conservation of sensitive species and ecosystems.

Vernal pools exemplify sensitive ecosystems that are often heavily grazed by livestock across broad areas within central and northeastern California, but that support diverse plant and animal communities and many rare and endemic species. Vernal pools are ephemeral wetlands that, due to California's Mediterranean climate, temporarily fill with

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winter precipitation and then dry during the long, hot summers. Vernal pool species are uniquely adapted to tolerate complete inundation in the winter and total desiccation during the summer months, with many having both aquatic and terrestrial phases in their life cycle (Keeley and Zedler 1998). Vernal pools across California have been extensively destroyed since the mid-1800s as a result of agricultural conversion and urban development (USDI 1997, 2005). It is estimated that 80–90% of the vernal pools historically present in California have been lost (Holland 1998). Many vernal pool specialist species have been federally listed as threatened or endangered (USDI 2005). Slender Orcutt grass (*Orcuttia tenuis* Hitchc.) is an annual grass species that grows only in vernal pools. It is federally listed as threatened and state listed in California as endangered due to its limited distribution and significant threats to its vernal pool habitat (USDI 1997; CDFW 2014). It is known to occur in approximately 100 locations in California, ranging from the Central Valley to the Modoc Plateau in northeastern California (USDI 2005).

When slender Orcutt grass was federally listed as threatened in 1997, grazing was considered one of the primary threats to this species, and many early status surveys of slender Orcutt grass focused on the potentially negative effects of livestock use (USDA and USDI 1989; USDI 1997). Although some authors had suggested that slender Orcutt grass may not be eaten by livestock because it produces a sticky, bitter-tasting exudate (Reeder 1982; Keeley 1998), this had not been proven. Concerns about both the potential direct and indirect effects of livestock use led federal land managers in northeastern California to permanently fence some sites supporting populations of slender Orcutt grass as early as 1988 (USDA and USDI 1989). However, research conducted in the Central Valley of California has demonstrated that removal of livestock can have negative consequences for a number of vernal pool specialist species (Marty 2005). Without grazing, plant litter can quickly accumulate and reduce light availability for vernal pool plant species. Marty (2005) found that excluding livestock reduced vernal pool inundation lengths by 50 — 80%, likely due to increased evapotranspiration, making it difficult for some vernal pool endemic species to complete their life cycles. Although the effect of livestock use on slender Orcutt grass has not been studied directly in the Central Valley, some authors have suggested that slender Orcutt grass may be tolerant of grazing (Stone et al. 1987). Declines in the number of other *Orcuttia* species, as well as negative trends in native vernal pool plant species abundance and richness, have been observed in Central Valley vernal pools after multiple seasons without grazing (Stone et al. 1987; Barry 1995; Griggs 2000; Marty 2005).

Based on findings suggesting positive effects of livestock use on vernal pool species in general in the Central Valley, we hypothesized that livestock use would benefit slender Orcutt grass in northeastern California. To test this hypothesis, the effects of livestock use on slender Orcutt grass were investigated using a replicated, paired design across a range of environmental conditions and grazing management regimes. Frequency, density, cover, reproductive potential, and height of slender Orcutt grass was compared in plots where livestock had been excluded with plots where grazing occurred. We aimed to determine if slender Orcutt grass was directly grazed by livestock and, if not, to determine the mechanisms behind any indirect effects of livestock use on this species. A better understanding of livestock use effects on slender Orcutt grass would provide land managers with practical information to more effectively manage the vernal pools of northeastern California for the benefit of both livestock production and sensitive ecological resources.

2. Methods

2.1. Study Area

Effects of livestock use were evaluated at 20 vernal pools supporting slender Orcutt grass in northeastern California. Vernal pools in northeastern California are located within the Great Basin floristic province, surrounded by low sagebrush (*Artemisia arbuscula* Nutt.), big sagebrush (*Artemisia tridentata* Nutt.), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), and western juniper (*Juniperus occidentalis* Hook) woodlands. Compared with vernal pools in the Central Valley, herbaceous plants are a smaller component of this vegetation type, and grasses that occur here are generally native perennial species. Vernal pools in northeastern California can span hundreds of hectares and are often filled by snow, precluding livestock use during the winter months (Keeler-Wolf et al. 1998). In the Central Valley, livestock use of vernal pools occurs between November and May, when most pools are still inundated, while in northeastern California livestock use occurs primarily during the dry summer months when vernal pool plant species are more likely to be grazed directly.

Study sites were located on public land managed by the Lassen National Forest (NF; $n = 8$), Modoc NF ($n = 11$), and the Alturas Field Office of the BLM (BLM; $n = 1$), ranging in elevation from 1067 to 1676 meters (m, Table 1). All study sites experience a montane Mediterranean climate, receiving an annual average of 47 cm of precipitation from 1923 to 2012 (WRCC 2012). Analysis of weather station and PRISM data showed interannual variability in both the total amount and timing of precipitation at each vernal pool (WRCC 2012; PRISM Climate Group 2015). However, precipitation was not measured directly for this study, and we did not have fine scale enough data to include precipitation in our models.

2.2. Experimental Design

Study sites included five vernal pools on the Lassen NF and Alturas Field Office of the BLM that had been fenced beginning as early as 1991 and four vernal pools on the Lassen NF that were open to livestock use. On the Modoc NF, 11 temporary electric fences were installed within vernal pools. Macroplots were established at each site, including paired unfenced and fenced macroplots on the Modoc NF. Our study included a total of 15 unfenced and 16 fenced macroplots. Each macroplot consisted of five parallel 14-m transects located 5 m apart, encompassing 350 m^2 (0.035 ha). Seven 1-m^2 plots were placed at 2-m intervals along each transect for a total of 35 plots per macroplot. A 0.2-m^2 frequency frame was nested within each 1-m^2 plot. All plots were located more than 2 m from fences to minimize edge effects.

In each 1-m^2 plot, all plant species were identified and a visual estimation was made of percent cover according to Daubenmire (1959) cover classes. Nomenclature of identified plant species followed Baldwin et al. (2012). Percent cover was also estimated for ground cover variables including herbaceous species, litter, rock, livestock hoofprints, livestock scat, and bare ground. The presence or absence of slender Orcutt grass and the number of slender Orcutt grass plants, if present, were evaluated within the 0.2-m^2 frequency frame. We measured the height and counted the number of spikelets of the closest slender Orcutt grass plant to the northeast corner of the 1-m^2 plot. Reproductive potential was estimated by multiplying spikelet number by plant number. Density and reproductive potential were calculated as plants $\cdot$ m^{-2} and spikelets $\cdot$ m^{-2}. A qualitative assessment of percent herbivory was made using the Landscape Appearance method (USDI 1999). In plots that showed evidence of herbivory, we identified the species grazed and estimated the amount of herbivory (percent cover grazed) each species had experienced.

Our experimental design consisted of repeated measurements for 3 years; however, not all sites could be sampled in all years due to time limitations. Unfenced macroplots varied in the type of livestock (sheep or cattle), season of grazing, and number of animal unit months (AUMs). Specific dates of livestock release and removal from pastures varied over the 3 years of our study. However, all sites could be generally grouped into one of three grazing seasons: 1) early, with livestock turned out in early June and removed before August; 2) late, with livestock released after July and removed by October; and 3) all season,

Table 1
Vernal pool study sites, including site name, location, elevation (m), fencing status, yr fenced, type of livestock, animal unit month (AUM), and season of grazing.

Site name	Location[1]	Elevation (m)	Fencing status[2]	Yr fenced[3,4]	Livestock[4]	AUM[4,5]	Season[4,6]
Adobe North	LNF	1 097	Fenced	1991	__	__	__
Fort Mountain	LNF	1 035	Fenced	2007	__	__	__
Grassy Lake	LNF	1 463	Paired plots	__	Cattle	135	Late
Green Place	BLM	1 038	Fenced	2001	__	__	__
Hackamore North	MDF	1 426	Paired plots	__	Sheep	1 915-2 471	All
Hackamore South	MDF	1 427	Paired plots	__	Sheep	1 915-2 471	All
Henski	MDF	1 459	Unfenced	__	Cattle	116-304	All
Highway 139	MDF	1 493	Paired plots	__	Cattle	110-250	Late
Little Bunchgrass Meadow[7]	LNF	1 602	Ungrazed	2004	__	__	__
McKay North	MDF	1 461	Paired plots	__	Cattle	291-372	Early
McKay South	MDF	1 462	Paired plots	__	Cattle	291-372	Early
Mud Lake	MDF	1 431	Paired plots	__	Cattle	__[8]	__[8]
Northeast Coyote Springs	LNF	1 521	Paired plots	__	Cattle	345-413	Early
Southeast Ebey Lake	LNF	1 706	Unfenced	__	Cattle	110-250	Late
South Whalen	MDF	1 331	Fenced	2009	__	338-605	__
Spaulding	MDF	1 453	Paired plots	__	Cattle	116-304	All
Spaulding West	MDF	1 451	Paired plots	__	Cattle	116-304	All
Swain Mountain	LNF	1 767	Unfenced	__	Cattle	100-199	Late
Tamarack Flat	LNF	1 645	Unfenced	__	Cattle	338-605	Late
Whitney Reservoir	MDF	1 427	Paired plots	__	Sheep	1 915-2 471	All

[1] LNF, MDF, and BLM indicate Lassen National Forest, Modoc National Forest, and Bureau of Land Management, respectively.
[2] Sites with paired plots had both fenced and unfenced treatments in the same vernal pool. Information on type of livestock, AUM, and season of grazing for paired plot sites refer to unfenced treatments only.
[3] Temporary electric fencing was installed at all sites with paired plots before the grazing season in 2010, except for Grassy Lake, where permanent paired plots were installed in 1997.
[4] ___, Type of livestock, AUM, and season of grazing is not applicable at fenced sites. Yr fenced is not applicable at grazed sites.
[5] AUM is shown as a range where values varied over the 3 yr of our study. Sheep and cattle AUM are not directly comparable.
[6] Season of grazing is defined as: a) early, with livestock removed before August, b) late, with livestock released after July, and c) all season, where livestock remain on pastures throughout the season.
[7] Little Bunchgrass Meadow is not fenced but has not been grazed by livestock since 2004.
[8] AUM and timing of grazing information were not available for Mud Lake.

where livestock were turned out in early June and left on pastures through October.

3. Statistical Analyses

3.1. Research Questions

Our analysis focused on answering four separate questions. 1) Do livestock graze slender Orcutt grass directly? 2) How did variables associated with livestock use management (fencing, time since fenced, season of grazing, and type of livestock) affect slender Orcutt grass response variables (frequency, density, cover, reproductive potential, and height)? 3) What environmental variables (herbaceous, bare ground, rock, litter, livestock hoofprint, and livestock scat cover) had a significant effect on slender Orcutt grass response variables? 4) How were environmental predictor variables identified as being related to slender Orcutt response variables (Question #3) in turn influenced by livestock management? By answering these four questions, we hoped to discover how livestock use affects slender Orcutt grass and identify potential mechanisms for any observed effects.

3.2. Analysis Approach

Our study included 11 sites where two macroplots occurred at the same site (paired fenced and unfenced macroplots) and 9 sites with single macroplots, where entire pools were fenced or unfenced (unpaired). To compare paired and unpaired macroplots, we used generalized linear mixed models (GLMMs) to include site as a random effect (i.e., random intercept terms) in our models to address potentially correlated responses associated with site locations. Plots were also included as random effects (nested within sites) in all models to account for correlated measurements among plots within the same site. All analyses were conducted in JMP 11.2 (SAS Institute Inc. 2013).

The use of GLMMs allowed us to retain the information within each plot without averaging, where valuable information may be lost, while also avoiding pseudoreplication (Bolker 2009). Analysis at the plot level was necessary because we did not manipulate grazing intensity, and almost 70% of plots outside the fenced exclosures had almost no evidence of livestock use. Most of the predictor variables associated with livestock use (percent cover of livestock hoofprints, livestock scat, bare ground, herbaceous species, litter and percent herbivory) varied considerably at the level of individual plots within macroplots. However, this analytical approach increased our sample size and may have exaggerated the statistical significance of some of the results. Therefore, results are interpreted using effect sizes rather than focusing on statistical significance. Effect sizes from GLMMs are reported as either the difference between predicted means (±95% confidence intervals) for each level of categorical predictor variables or as parameter estimates (±95% confidence intervals) for models containing continuous predictor variables. Although some effect sizes are expressed as percentages (for variables measured in percentage units such as cover), they represent absolute (percentage point) differences in predicted values and not relative values. Descriptive results are reported as means ± standard error.

We included year as a fixed effect in our analyses. We felt year was an important variable for several reasons: 1) slender Orcutt grass is an annual plant that has been observed to exhibit large annual population fluctuations; 2) hydrologic conditions of vernal pools depend heavily on annual patterns of precipitation; and 3) a number of other climatic variables varied annually. We interpreted the "year effect" as a covariate to statistically control for various known (e.g., precipitation) and unknown sources of interannual variability, allowing more precise inferences concerning the livestock use — related effects of interest.

3.3. Effects of Livestock Use on Slender Orcutt Grass

To determine if livestock directly herbivorize slender Orcutt grass, herbivory data were summarized by species. To evaluate the effect of fencing on slender Orcutt grass responses, including frequency, density, percent cover, reproductive potential, and height, all 16 fenced macroplots were compared with all 15 unfenced macroplots. GLMMs with plots nested within sites specified as hierarchical random effects and fencing status and year specified as fixed effects were used. To evaluate the effect of installing fenced exclosures at each of the 11 individual study sites with paired macroplots (fenced and unfenced), two-way analysis of variance (ANOVA) was used. Year and fencing status were the two independent variables in these analyses, and frequency, density, percent cover, reproductive potential, and height of slender Orcutt grass were the dependent variables. Post hoc comparisons of mean differences were conducted using Tukey's honest significant difference (HSD) tests.

Analysis of the effect of time since fenced on slender Orcut grass responses used all 16 fenced macroplots. Again, GLMMs were used, with plots nested within sites specified as random effects and time since fenced (years) specified as a fixed effect. Analysis of the effect of type of livestock (sheep vs. cattle) also used all 16 fenced macroplots in GLMMs, with plots nested within sites specified as random effects and type of livestock and year specified as fixed effects. Analysis of the effect of season of grazing used the 13 cattle-grazed macroplots only because sheep-grazed pastures were grazed throughout the season.

3.4. Effects of Environmental Variables on Slender Orcutt Grass

To identify environmental variables that had a significant effect on slender Orcutt grass responses, we used step-wise model selection based on minimum Akaike information criterion (AIC). Middle points of Daubenmire cover classes were used for cover of livestock hoofprints, bare ground, herbaceous species, litter, rock, and year. Variables that did not improve AIC for models of cover, density, frequency, and reproductive potential were dropped, including rock, livestock scat, and herbaceous cover. Variables dropped from the final model of slender Orcutt grass height included bare ground, livestock hoofprints, and litter cover. Pearson's correlation coefficients between all selected environmental variables were below 0.4, and variance inflation factors were below 2. Final models of selected variables and slender Orcutt grass responses were again fit using GLMMs with plots nested within sites specified as random effects.

3.5. Effects of Livestock Use on Environmental Predictor Variables

To determine how the environmental predictor variables identified by model selection using AIC (described in section 3.4) were in turn influenced by livestock use (fencing, time since fenced, season of grazing, and type of livestock) and year, we again used GLMMs with plots nested with sites specified as random effects. Macroplots used for these analyses are as described earlier for the analysis of the effect of livestock use (section 3.3, Effects of Livestock Use on Slender Orcutt Grass).

4. Results

4.1. Descriptive Results

Slender Orcutt grass was present in 60% of our 0.2-m^2 frequency frames, with a mean density of 20 plants · m^{-2} and a mean reproductive potential of 475 spikelets · m^{-2}. Mean cover was 7%, and mean plant height was 60 mm. However, there was great variability among macroplots. Frequency ranged from 3% to 98%, density ranged from 0 to 240 plants · m^{-2}, cover ranged from 0.5% to 26%, reproductive potential ranged from 0 to 1 215 spikelets · m^{-2}, and height varied from 26 to 122 mm. Slender Orcutt grass response variables also varied considerably from year to year; mean frequency, density, and cover were highest in 2009 and lowest in 2010, while reproductive potential and plant height were highest in 2011. Mean frequency was 78 ($\pm$2)% in 2009 but only 39 ($\pm$2)% in 2010. Mean density was 81 ($\pm$4) plants · m^{-2} in 2009 but fell to 20 ($\pm$2) plants · m^{-2} in 2010. Mean cover was 11 ($\pm$1)% in 2009 but only 3.0 ($\pm$0.3)% in 2010. Reproductive potential was 657 ($\pm$31) spikelets · m^{-2} in 2011 and 296 ($\pm$27) spikelets · m^{-2} in 2010. Plant height varied from a mean of 70 ($\pm$1) mm in 2011 to 44 ($\pm$1) mm in 2009.

Measured environmental variables, including percent cover of herbaceous species, bare ground, litter, livestock hoofprints, and livestock scat, also varied between macroplots. Herbaceous cover ranged from 13% to 64%, bare ground cover from 5% to 49%, litter cover from 2% to 32%, rock cover from 0% to 21%, livestock scat cover from 0% to 2%, and livestock hoofprint cover from 0% to 13%. All ground cover variables, except rock cover, also varied greatly between the 3 years of our study (2009–2011). Herbaceous cover ranged from 47 ($\pm$1)% in 2009 to 32 ($\pm$1)% in 2010; livestock hoofprint cover from 4.5 ($\pm$0.3)% in 2011 to 0.8 ($\pm$0.1)% in 2009, livestock scat cover from 0.40 ($\pm$0.05)% in 2009 to 0.08 ($\pm$0.01)% in 2011, litter cover from 21 ($\pm$1)% in 2009 to 10 ($\pm$1)% in 2011, and bare ground cover from 34 ($\pm$1)% in 2009 to 25 ($\pm$1)% in 2011.

4.2. Direct Effects of Livestock Use on Slender Orcutt Grass

Evidence of livestock use was generally low across our study sites. Almost 70% of plots outside the fenced exclosures showed limited evidence of grazing (<5% plant cover grazed). More than 60% of plant cover was used by livestock in only 12 plots (<1%). However, evidence of herbivory was 10.0 ($\pm$0.4)% in unfenced plots compared with 4.5 ($\pm$0.3)% in fenced plots, livestock hoofprint cover was 1.5 ($\pm$0.2)% in fenced plots compared with 3.5 ($\pm$0.2)% in unfenced plots, and livestock scat cover was 0.13 ($\pm$0.02)% in fenced plots compared with 0.30 ($\pm$0.03)% in unfenced plots. These differences indicate that fencing was effective at reducing livestock use. The most commonly grazed species were perennial graminoids, many of which were grazed up to twice as often as predicted by their availability; we did not find evidence of herbivory of slender Orcutt grass (Table 2).

4.3. Indirect Effects of Livestock Use on Slender Orcutt Grass

The indirect effects of livestock use on slender Orcutt grass were apparent in only some years (Fig. 1). In 2009, slender Orcutt grass was 27 ($\pm$12)% more frequent, density was 55 ($\pm$20) plants · m^{-2} greater, and cover was 7.5 ($\pm$3)% higher in unfenced plots. In 2010, when frequency, density, and cover were low, these responses did not differ between fenced and unfenced plots. In 2011, frequency was 11 ($\pm$4)% higher and density was 15 ($\pm$3) plants · m^{-2} greater in unfenced plots, while percent cover did not differ between fenced and unfenced plots. Reproductive potential was not influenced by fencing status. On average, slender Orcutt grass was 27 mm ($\pm$4 mm) taller in unfenced plots.

We found declines in slender Orcutt grass frequency, density, cover and reproductive potential with time since fencing (Table 3). For every 10 years of exclusion from livestock, frequency declined by 12 ($\pm$5)%, density by 30 ($\pm$10) plants · m^{-2}, cover by 3.3 ($\pm$1.3)%, and reproductive potential by 120 ($\pm$90) spikelets · m^{-2}. On the other hand, slender Orcutt grass height increased by 41 mm ($\pm$4 mm) with every decade since fencing.

Slender Orcutt grass responses also varied among pastures grazed during different seasons (Fig. 2). Frequency was 20 ($\pm$13)% lower, and there were 48 ($\pm$22) fewer plants m^{-2} in pastures grazed early in the season compared with those grazed late in the season. Cover was 8.5 ($\pm$3.5)% lower in early-season pastures than in late-season pastures. Height was 20 ($\pm$11) mm lower in early-season than late-season pastures. Reproductive potential was 500 ($\pm$250) spikelets · m^{-2} lower in early-season compared with late-season pastures.

Frequency, density, cover, reproductive potential, and height of slender Orcutt grass differed in pastures grazed by cattle compared with those grazed by sheep, but the direction and magnitude of this effect varied by year (Fig. 3). There were on average 60 ($\pm$23) fewer plants · m^{-2}, 10 ($\pm$3)% lower areal cover, and 410 ($\pm$160) fewer spikelets · m^{-2}, and plants were 10 ($\pm$5) mm shorter in cattle-

Table 2
Species eaten by livestock, including their functional group, availability, utilization, and preference.

Scientific name	Functional group	Availability (% cover in plot)	Utilization (% of total grazed)	Preference[1]
Juncus mexicanus	Perennial graminoid	0.8	1.8	2.1
Muhlenbergia richardsonis	Perennial graminoid	3.3	6.7	2.1
Juncus nevadensis	Perennial graminoid	26.6	53.0	2.0
Alopecurus geniculatus	Perennial graminoid	3.0	5.6	1.9
Eleocharis macrostachya	Perennial graminoid	5.8	10.0	1.7
Eryngium mathiasiae	Perennial forb	4.3	6.5	1.5
Juncus hemiendytus	Annual graminoid	0.5	0.7	1.4
Eleocharis parishii	Perennial graminoid	1.5	1.8	1.2
Alopecurus saccatus	Annual graminoid	0.5	0.6	1.1
Elymus smithii	Perennial graminoid	4.2	3.7	0.9
Eryngium articulatum	Perennial forb	13.1	6.1	0.5
Downingia bicornuta	Annual forb	1.5	0.6	0.4
Orcuttia tenuis	Annual graminoid	7.2	0	0

[1] Preference calculated as utilization/availability.

grazed pastures compared with sheep-grazed pastures in 2009. Frequency did not differ between sheep- and cattle-grazed pastures in 2009. However, in 2010 the effect of cattle grazing (vs. sheep grazing) was to increase frequency by 9 ($\pm$3)%, cover by 5.2 ($\pm$0.8)%, spikelet density by 265 ($\pm$37) spikelets $\cdot$ m^{-2}, and grass height by 16 ($\pm$10) mm. There was no difference in slender Orcutt grass density between cattle- and sheep-grazed pastures in 2010.

Of the 11 sites with paired unfenced and fenced macroplots, slender Orcutt grass exhibited positive responses to livestock use at 9 sites; negative responses were found at only 2 sites. Frequency was 5.7 ($\pm$2.8)% lower in unfenced plots at McKay North. Cover was 4.5 ($\pm$1.9)% lower, and reproductive potential was 17 ($\pm$6) spikelets $\cdot$ m^{-2} lower in unfenced plots at Spaulding. These two sites had the lowest mean litter cover of all our study sites (2% compared with site-wide mean of 16%), and the highest cover of livestock hoofprints (10% compared with site-wide mean of 2%).

4.4. Effects of Environmental Variables on Slender Orcutt Grass

Model selection identified year as the variable that most strongly affected slender Orcutt grass responses. However, increases in litter, bare ground, and livestock hoofprint cover also had effects on frequency, density, cover, and reproductive potential (Table 4). For every 10% increase in bare ground cover, frequency decreased by 2.2 ($\pm$0.7)%, density decreased by 5.7 ($\pm$1.3) plants $\cdot$ m^{-2}, cover decreased by 1.2 ($\pm$0.2)%, and reproductive potential decreased by 41 ($\pm$15) spikelets $\cdot$ m^{-2}. A 10% increase in litter cover resulted in a 2.0 ($\pm$0.9)% decrease in frequency, an 8.0 ($\pm$1.5) plants $\cdot$ m^{-2} decrease in density, a 1.3 ($\pm$0.3)% decrease in cover, and a 158 ($\pm$51) spikelets $\cdot$ m^{-2} decrease in reproductive potential. A 10% increase in livestock hoofprint cover was associated with a 6.0 ($\pm$2.4)% decrease in frequency, a 16 ($\pm$4) plants $\cdot$ m^{-2} decrease in density, a 2.8 ($\pm$0.6)% decrease in cover, and a 32 ($\pm$10) spikelets $\cdot$ m^{-2} decrease in reproductive potential. Slender Orcutt grass height was strongly affected by year and positively associated with herbaceous and rock cover (see Table 4). A 10% increase in herbaceous cover was associated with a 2.9 ($\pm$0.6)-mm increase in height, and a 10% increase in rock cover with a 6.2 ($\pm$1.4)-mm increase in height.

4.5. Effects of Livestock Use on Environmental Predictor Variables

Of the environmental variables that were associated with slender Orcutt grass frequency, density, cover, and reproductive potential (see previous section), only litter cover was affected by both year and grazing status (Fig. 4). Litter cover was 20 ($\pm$6)% higher in fenced plots compared with unfenced plots in 2009, 5.5 ($\pm$3.4)% lower in fenced

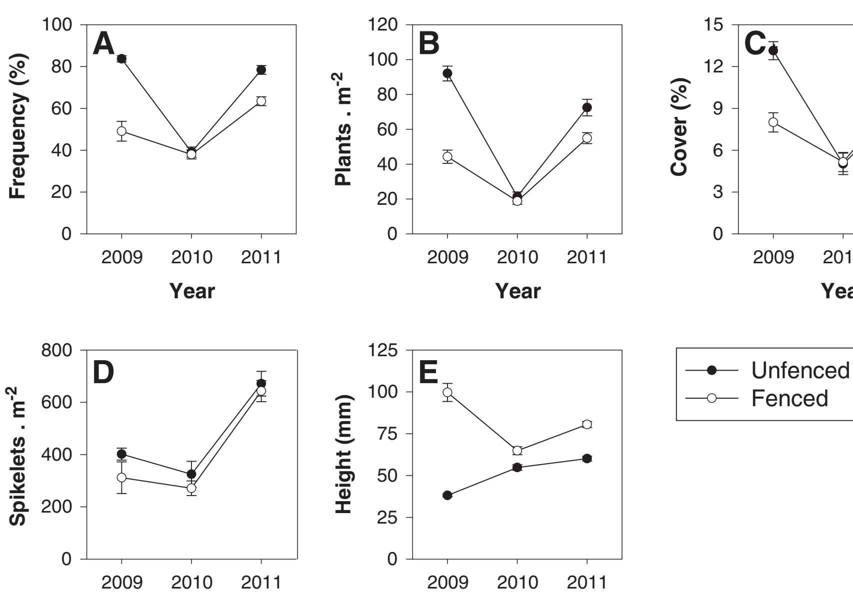

Figure 1. The effect of fencing on slender Orcutt grass responses differed by year. **A,** Frequency. **B,** Density. **C,** Cover. **D,** Reproductive potential. **E,** Height. Error bars are standard error.

Table 3
Parameter estimates of the associations among slender Orcutt grass frequency, density, cover, reproductive potential, and height with time since fencing (yr). All 16 fenced macroplots were included in this analysis using generalized linear mixed models, with plots nested within sites specified as random effects.

Variable	Parameter[1]	Estimate	Standard error	Lower 95% CI[2]	Upper 95% CI[2]	Model $R^{2(3)}$
Frequency (%)	Intercept	61.29	1.35	58.65	63.93	0.58
	Time Since Fenced	−1.23	0.28	−1.78	−0.68	
Density (plants · m^{-2})	Intercept	57.87	2.29	53.38	62.36	0.57
	Time Since Fenced	−3.07	0.48	−4.00	−2.13	
Cover (%)	Intercept	7.75	0.29	7.17	8.32	0.27
	Time Since Fenced	-0.33	0.06	−0.46	−0.21	
Reproductive potential (spikelets · m^{-2})	Intercept	496.54	20.04	457.11	535.97	0.29
	Time Since Fenced	−12.10	4.51	−20.95	−3.25	
Height (mm)	Intercept	53.04	0.78	51.51	54.57	0.31
	Time Since Fenced	4.05	0.18	3.71	4.40	

[1] Time since fenced measured in yr.
[2] Confidence interval.
[3] Adjusted coefficient of determination.

plots in 2010, and 3.3 (±1.2)% higher in fenced plots in 2011. Other environmental variables that were related to slender Orcutt grass frequency, density, cover, and reproductive potential—bare ground and livestock hoofprint cover—were 5.4 (±2.3) and 2.5 (±0.5)% higher in unfenced plots, respectively, and this pattern did not vary between years. Herbaceous cover, positively associated with slender Orcutt grass height, was 6.6 (±0.8)% higher in fenced plots in all years. As expected, rock cover did not differ between unfenced and fenced plots.

Cover of bare ground declined by 18 (±3)%, and livestock hoofprints declined by 2.1 (±0.5)% for every 10 years of fencing. Litter increased by 5.8 (±1.9)% and herbaceous cover increased by 15 (±3)% for every 10 years of livestock exclusion.

Environmental variables associated with slender Orcutt grass responses, including bare ground, herbaceous, and livestock hoofprint cover also varied according to season of grazing (Fig. 5). Livestock hoofprints were 7.9 (±1.8)% higher, and herbaceous species cover was 10 (±3)% lower in early-season pastures compared with those grazed late in the season. Bare ground cover was 25 (±4)% lower in late-season pastures compared with those grazed all season. Litter cover did not vary with season of grazing.

Environmental variables that affected slender Orcutt grass frequency, density, cover, and reproductive potential, including litter, bare ground, and livestock hoofprint cover, differed in pastures grazed by cattle compared with those grazed by sheep (see Table 4, Fig. 6). Litter cover was 14 (±2)% lower, while bare ground and livestock hoofprint cover were 10 (±3) and 2.0 (±0.5)%, respectively, higher in pastures grazed by cattle. The environmental variable most strongly related to slender Orcutt grass height, herbaceous cover, was 8.7 (±3.2)% higher in sheep-grazed pastures compared with those grazed by cattle.

5. Discussion

We found no evidence that livestock consume slender Orcutt grass. Other authors have suggested that slender Orcutt grass is unpalatable to most grazing herbivores, probably as a result of a sticky, bitter-tasting exudate that may serve as a biochemical herbivory avoidance strategy (Reeder 1982; Keeley 1998). Our study confirms this observation. However, despite the fact that livestock do not graze slender Orcutt grass directly, our results suggest that livestock use can still have important indirect effects on this species.

Overall, the effects of livestock use on slender Orcutt grass were small compared with the effect of year, and in some years livestock use had no effect (see Fig. 1). Slender Orcutt grass responses varied greatly during the 3 years of our study. Large annual fluctuations in slender Orcutt grass population sizes have been frequently reported and are likely the result of differences in precipitation patterns (amount, timing, and rain vs. snow) that alter the hydrologic regime of vernal pools, including pool depth and length of inundation (Griggs and Jain 1983; Holland and Jain 1984; Holland 1987; Stone et al. 1987; USDA and USDI 2012). Studies have shown that the effects of grazing on plant

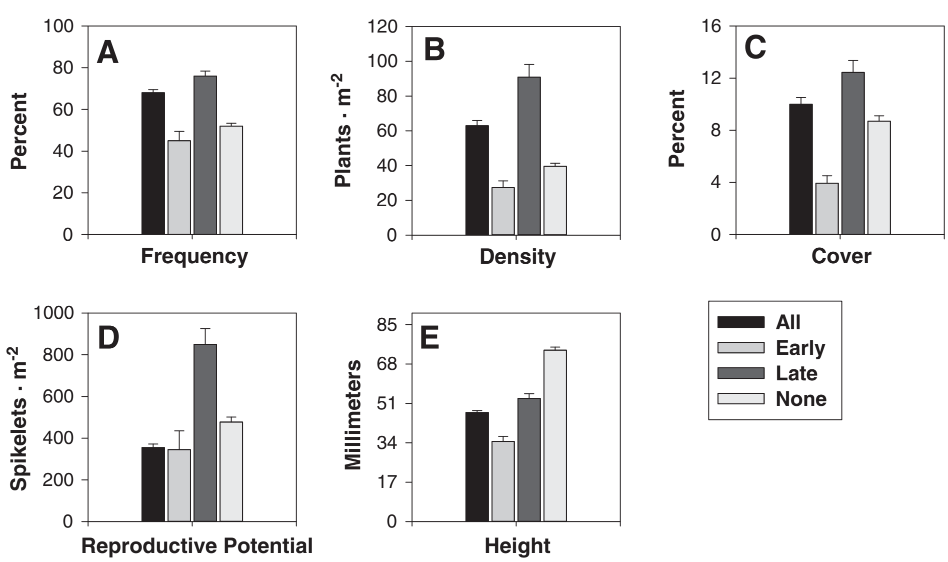

Figure 2. Slender Orcutt grass responses differed according to season of grazing (All, Early, Late, or None). **A,** Frequency. **B,** Density. **C,** Cover. **D,** Reproductive potential. **E,** Height. Error bars are standard error.

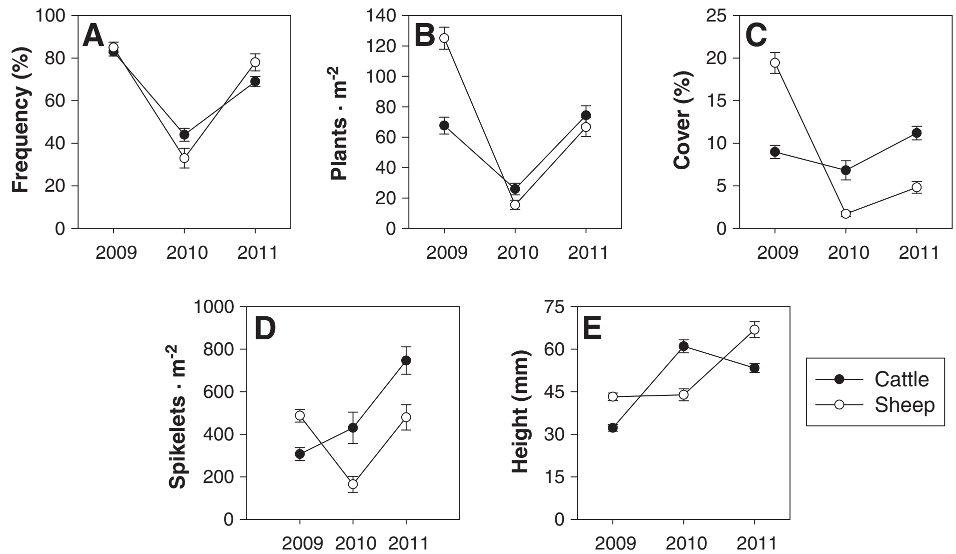

Figure 3. Slender Orcutt grass responses varied according to type of livestock (sheep or cattle) and year. **A,** Frequency. **B,** Density. **C,** Cover. **D,** Reproductive potential. **E,** Height. Error bars are standard error.

community structure in Mediterranean herbaceous communities are stronger in wet years than in dry years, especially if the plant life cycle is closely tied to patterns of rainfall and hydrologic regime (Sternberg et al. 2000).

Our results suggest that the effects of livestock use on slender Orcutt grass are complex, including both positive, neutral, and negative effects. In years when slender Orcutt grass was abundant, we found that livestock use resulted in increased frequency, density, and cover of slender Orcutt grass (see Fig. 1). Although livestock use had no effect on slender Orcutt grass in some years, we found declines in slender Orcutt grass frequency, density, cover and reproductive potential over time after exclusion from livestock use (see Table 3). This suggests that despite interannual variability in the effects of livestock use, over longer time periods a lack of grazing can be detrimental to slender Orcutt grass.

We found that livestock use can benefit slender Orcutt grass in northeastern California, although this effect depended strongly on both year and season of grazing (see Fig. 2). Grazing reduced litter cover in some years (see Fig. 4). As litter cover decreased, slender Orcutt

Table 4
Parameter estimates of the associations among slender Orcutt grass frequency, density, cover, reproductive potential, and height with selected environmental variables. Generalized linear mixed models with plots nested within sites specified as random effects.

Variable	Parameter[1]	Estimate	Standard error	Lower 95% CI[2]	Upper 95% CI[2]	Model R^2[3]
Frequency (% of plots)	Intercept	70.52	1.88	66.85	74.20	0.72
	Bare ground	−0.22	0.04	−0.29	−0.15	
	Litter	−0.20	0.04	−0.29	−0.11	
	Hoofprint	−0.60	0.12	−0.83	−0.36	
	Yr [2009]	16.05	1.04	14.02	18.08	
	Yr [2010]	−23.66	0.95	−25.53	−21.79	
Density (plants · m^{-2})	Intercept	85.81	3.23	79.48	92.14	0.71
	Bare ground	−0.57	0.06	−0.70	−0.45	
	Litter	−0.80	0.08	−0.95	−0.65	
	Hoofprint	−1.58	0.21	−1.99	−1.17	
	Yr [2009]	31.58	1.81	28.03	35.13	
	Yr [2010]	−36.43	1.67	−39.70	−33.16	
Cover (%)	Intercept	13.53	0.49	12.56	14.49	0.49
	Bare ground	−0.12	0.01	−0.14	−0.10	
	Litter	−0.13	0.01	−0.16	−0.11	
	Hoofprint	−0.28	0.03	−0.35	−0.22	
	Yr [2009]	5.19	0.31	4.58	5.81	
	Yr [2010]	−5.28	0.29	−5.84	−4.72	
Reproductive potential (spikelets · m^{-2})	Intercept	681.49	36.54	609.83	753.15	0.40
	Bare ground	−4.07	0.77	-5.59	-2.55	
	Litter	−15.81	2.59	-20.90	-10.73	
	Hoofprint	−3.162	0.5185	-4.179	-2.145	
	Yr [2009]	−7.17	22.76	-51.83	37.49	
	Yr [2010]	−185.01	23.09	-230.31	-139.71	
Height (mm)	Intercept	45.24	1.47	42.35	48.13	0.55
	Visit_Yr [2009]	−14.82	0.95	−16.68	−12.96	
	Visit_Yr [2010]	0.91	0.97	−0.99	2.80	
	Rock Cover	0.62	0.07	0.48	0.77	
	Herb Cover	0.29	0.03	0.23	0.35	

[1] Hoofprints, litter, bare ground, herb, and rock parameters are percent cover.
[2] Confidence interval.
[3] Adjusted coefficient of determination.

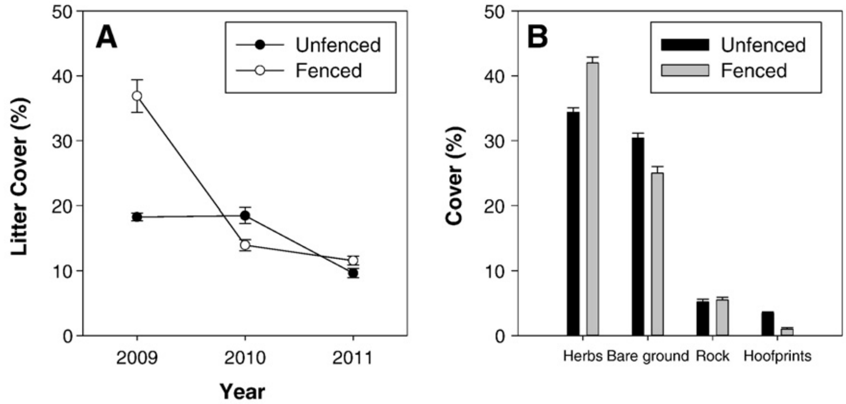

Figure 4. The effect of fencing status and year on environmental variables. **A,** Litter cover differed by year and fencing status. **B,** Other environmental variables (herbaceous, bare ground, and livestock hoofprint cover) differed by fencing status alone. Rock cover was not affected by fencing status. Error bars are standard error.

grass frequency, density, cover, and reproductive potential increased (see Table 4). Litter cover can act as a physical barrier to the growth and establishment of most annual plants, which require light and access to soil for establishment (Facelli and Pickett 1991). Land managers and scientists interviewed by Robins and Vollmar (2002) cited the accumulation of litter as the primary management concern for maintaining vernal pool flora. In the Central Valley, where cover of non-native grasses can exceed 80%, it is not surprising that litter would accumulate without grazing. However, our results suggest that even in northeastern California, where the uplands surrounding vernal pools are much less frequently invaded by non-native grasses, reduction of litter in unfenced plots was associated with increased frequency, density, cover, and reproductive potential of slender Orcutt grass.

Slender Orcutt grass plants were also shorter in unfenced plots, and these plots had lower herbaceous cover. Plant height increased over time in fenced pastures. Although livestock do not directly graze slender Orcutt grass, plants growing in fenced sites may experience more competition for light, causing them to grow taller (Belsky 1992). Greater carbon allocation to height growth may have come at the expense of reproductive output, which decreased over time in fenced pastures (Obeso 2002). Livestock use may also benefit slender Orcutt grass by altering variables we did not measure, such as vernal pool hydrology. Marty (2005) found that release from grazing reduced pool inundation lengths by 50% to 80%, making it difficult for some endemic vernal pool species to complete their life cycles. Shorter inundation periods may have resulted from lower evapotranspiration rates in pools that had been grazed where the abundance of vegetation, primarily grasses, was lower (Marty 2005).

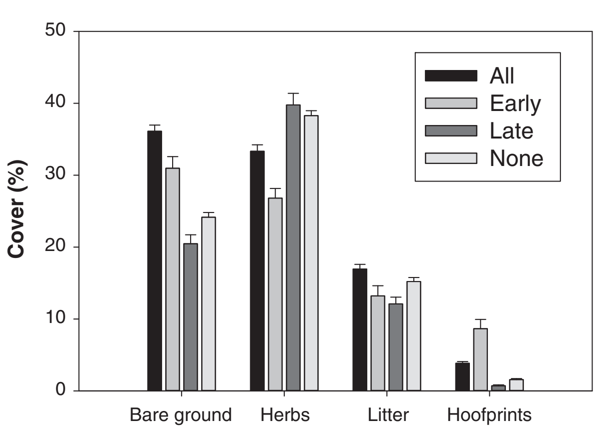

Figure 5. Bare ground, herbaceous, litter, and livestock hoofprint cover varied with season of grazing (All, Early, Late or None). Error bars are standard error.

Conversely, we found that livestock use can also negatively affect slender Orcutt grass. Frequency, density, cover, and reproductive potential of slender Orcutt grass were lower where livestock hoofprint and bare ground cover was high (see Table 4). Although it has been suggested that hoofprints create microtopographic depressions or compacted soils that could benefit slender Orcutt grass by extending pool inundation lengths (Pyke and Marty 2005), we found that individual study sites with the highest cover of livestock hoofprints and bare ground were also the sites where paired plot data demonstrated negative effects of livestock use on frequency, cover, and reproductive potential. Similarly, pastures that were grazed early in the season had the highest cover of livestock hoofprints (see Fig. 5), and early-season grazing had negative effects on slender Orcutt grass frequency, density, and cover (see Fig. 2). Livestock hoofprints may be more destructive early in the season when vernal pool soils are moist, and trampling may be more detrimental to slender Orcutt grass during the early stages of its life cycle, preventing plants from setting seed (Stone et al. 1987; Griggs 2000; Robins and Vollmar 2002). On the other hand, pastures grazed late in the season, which had lower livestock hoofprint and bare ground cover, had the highest slender Orcutt grass density, cover, and reproductive potential of all sites.

We found that slender Orcutt grass responses differed between sheep- and cattle-grazed pastures; however, the magnitude and direction of these differences varied by year (see Fig. 3). Most responses were higher in sheep-grazed pastures when slender Orcutt grass was abundant but lower in these pastures in unproductive years. Although sheep and cattle AUM are not directly comparable, average AUM was 2 193 in sheep-grazed pastures and 269 in cattle-grazed pastures, suggesting that differences in grazing intensity were not responsible for these patterns. Instead, differences in the way sheep and cattle affect slender Orcutt grass may be related to not only differences in the foraging behavior of these animals but also to annual variability in productivity. Litter cover was higher in sheep-grazed pastures, while bare ground and livestock hoofprint cover were higher in pastures grazed by cattle (see Fig. 6). Sheep may be preferable to cattle for maintaining slender Orcutt grass populations at highly disturbed sites because they expose less bare ground and create fewer hoofprints than cattle. On the other hand, we found that sheep were less effective than cattle at removing litter and reducing the cover of herbaceous species, suggesting that cattle grazing may be preferable at sites, or during years, where cover of herbaceous species is high. Cattle are true grazers and show strong preferences for grasses (Grant et al. 1985). However, both sheep- and cattle-grazed pastures had less litter than fenced sites, and in general the differences between these two types of livestock were small.

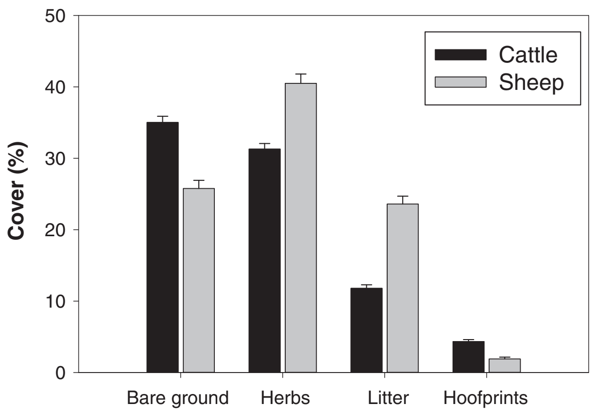

Figure 6. Bare ground, herbaceous, litter, and livestock hoofprint cover differed in pastures grazed by sheep compared with those grazed by cattle. Error bars are standard error.

6. Implications

Our results show that land managers can balance the needs of sensitive vernal pool habitats and species with the maintenance of livestock utilization on public lands. However, a grazing management plan that is compatible with the conservation of slender Orcutt grass populations should incorporate information concerning annual variability (including patterns of precipitation and productivity), season of grazing, and type of livestock. Managers might increase AUM in years when vernal pool plant productivity is high because livestock use can benefit slender Orcutt grass by reducing litter cover. Research in the Central Valley indicates this would benefit other vernal pool plant species as well (Stone et al. 1987; Barry 1995; Robins and Vollmar 2002; Marty 2005). Individual site conditions might also inform grazing management strategies. For example, sites that have been excluded from grazing for multiple years may benefit from the reintroduction of livestock, particularly where litter accumulation has occurred. On the other hand, sites that are highly disturbed and have very low litter cover may benefit from livestock exclusion, or grazing by sheep instead of cattle. Under any conditions, early-season grazing is not recommended for the maintenance of slender Orcutt grass populations, which are most resilient to grazing pressure after the initial stages of their annual life cycle are complete. The overriding effect of hydrologic regime on vernal pool plant communities, including slender Orcutt grass, suggests that efforts to maintain suitable habitat conditions, specifically by restoring the hydrology of vernal pools, may be more critical than grazing management to protect slender Orcutt grass and other vernal pool species in the region. Holland (2006) found that over one-third of the 660 vernal pools mapped on the Modoc NF had some evidence of hydrologic degradation such as ditching and damming. Predicted changes in temperature and patterns of precipitation and runoff in northeastern California may impact habitat suitability for vernal pool specialist plants (Pyke 2005), making efforts to restore vernal pool hydrology even more critical.

Our study was mostly observational, and most of our plots outside of fenced exclosures were not subject to livestock use. Future research that involves a manipulative experiment, for example by controlling grazing intensity, hoofprints, or litter cover, would help further elucidate the effect of livestock use on slender Orcutt grass. Additional research that compares slender Orcutt grass populations in the Central Valley with those in northeastern California, including an evaluation of differences in phenology, genetic variability, vernal pool morphology, and grazing management practices, would provide further insight into the factors that influence the effect of livestock use on this species across its range. Although we focused our investigation on a single species, slender Orcutt grass, other vernal pool plant species have highly specialized adaptations to the vernal pool environment and may be strongly influenced by annual variability in precipitation and other factors, as well as litter cover. A grazing management plan designed to maintain slender Orcutt grass and consider these variables will likely benefit other vernal pool plant species as well.

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