# Long-term Benefits to Vernal Pool Annuals May Outweigh Short-term Consequences of Livestock Grazing on the Modoc Plateau

KIRSTEN M. BOVEE

Lassen National Forest, U.S. Department of Agriculture, Forest Service
Chester, CA 98620
kirsten.bovee@usda.gov

KYLE E. MERRIAM

Sierra Cascade Province, U.S. Department of Agriculture, Forest Service
Quincy, CA 95971

MEREDITH C. GOSEJOHAN

Department of Natural Resources and Environmental Science,
University of Nevada, Reno, NV 89512

ABSTRACT. Snow-filled vernal pools on the high-elevation Modoc Plateau in northeastern California experience climatic conditions that differ from the better studied pools of the Central Valley, and lack the invasive species dominance observed in many ungrazed Central Valley pools. We asked whether these differences might translate into distinctions in livestock grazing effects to montane vernal pool plant communities. Our research found that over the long-term (i.e., >5 years), livestock grazing exclosures were associated with strong shifts in vernal pool species composition (Bovee et al., 2018). Long-term fenced pools averaged six times the cover of vernal pool perennials, but just a quarter the cover of vernal pool annuals relative to pools that were open to grazing. Patterns of livestock use within vernal pools suggest that livestock preferentially utilize vernal pool perennials as forage, consistent with reduced cover of this functional group with long-term fencing. However, short-term (year-to-year) effects of livestock grazing to vernal pool annuals were also significant and often contrasted with the effects observed over longer time periods. In areas where hoofprint cover or bare ground cover increased relative to previous years, the cover of vernal pool annuals declined. While vernal pool annuals may be susceptible to adverse grazing effects at small spatial scales, over the long-term, grazing confers a net benefit to this functional group under most grazing regimes on the Modoc Plateau. Evaluating the re-introduction of livestock grazing to fenced vernal pools should take into account the timing and intensity of grazing to maximize benefits to vernal pool annuals and perennials alike.

CITATION. Bovee, K.M., K.E. Merriam, and M.C. Gosejohan. 2019. Long-term benefits to vernal pool annuals may outweigh short-term consequences of livestock grazing on the Modoc Plateau. Pages 27-44 in R.A. Schlising, E.E. Gottschalk Fisher, C.M. Guilliams, and B. Castro (Editors), Vernal Pool Landscapes: Past, Present and Future. Studies from the Herbarium Number 20, California State University, Chico, CA.

## INTRODUCTION

The vernal pools of the Modoc Plateau are California's highest in elevation. They occur on northern basalt hardpan, and are fed primarily by snowmelt. Most montane vernal pools are not threatened by development or land use conversion or are managed for livestock grazing (USDA, FS, 2018). Until recent years, little was known about these montane vernal pools or how they may differ from better studied pools at lower elevations elsewhere in the state. Our recent work, however, has found that topographic and climatic differences translate into distinctive species composition and differences in how livestock grazing may affect these systems (Merriam et al., 2016; Gosejohan et al., 2017; Bovee et al., 2018).

Livestock effects to plant communities have been studied across a global range of habitat types (Díaz et al., 2007; Cingolani et al., 2005). The effects of livestock grazing may include increased bare ground cover, decreased litter accumulations, soil disturbance, and soil compaction. In combination, these effects can influence plant community composition and species diversity (Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998; Harrison et al., 2003; Díaz et al., 2007; Noy-Meir et al., 1989; Krausman et al., 2009). In general, annual species benefit from grazing pressure, particularly in wetter, more productive environments (Díaz et al., 2007). Although pools on the Modoc Plateau are nested in semiarid sagebrush or eastside pine environments (e.g., not wet and productive), vernal pool plant communities experience seasonal inundation and a different growing environment than the surrounding landscape.

In the Central Valley, livestock grazing has been used as an important management tool to reduce cover of robust, invasive annual grasses and associated thatch, resulting in increased native species diversity and extended pool hydroperiod (Pyke and Marty, 2005; Marty, 2015). However several key differences between low elevation and high elevation vernal pools led us to consider that livestock grazing effects in montane vernal pools needed to be evaluated separately. First, pools on the Modoc lack the dominant cover of robust, invasive annual grasses that contribute strongly to litter depth in lower elevation pools. Second, while Central Valley pools are filled by winter and spring rains, Modoc pools fill in late spring and early summer as snow melts. These climatic differences lead to differences in grazing timing. Central Valley pools are grazed while pools are still inundated, whereas livestock graze Modoc pools later in the season, most often after they have dried (Merriam et al., 2016).

While associated research has focused on the Federally Threatened species *Orcuttia tenuis* (Merriam et al., 2016), we were also interested in livestock grazing effects to vernal pool plant communities as a whole (see Bovee et al., 2018). Keeley and Zedler (1998) and Solomeshch et al. (2007) offered useful conceptual frameworks to divide vernal pool species into functional groups that distinguish between vernal pool specialists and more cosmopolitan wetland and upland species that can co-occur in vernal pool environments. While many genera are endemic or generally restricted to vernal pools, other genera occur across a broad range of wetland habitats such as wet meadows, marshes, or riparian areas. We were primarily interested in livestock grazing effects to vernal pool annuals (VA) vernal pool perennials (VP), and wetland perennials (WP) such as *Eleocharis macrostachya* that have been identified as potential competitors with rare annual vernal pool endemics such as *Orcuttia tenuis*.

We found that livestock grazing on the Modoc Plateau can have strong effects to the distributions of both vernal pool annuals and perennials (Bovee et al., 2018). Cover of vernal pool annuals declined with longer fencing duration, while cover of vernal pool perennials increased (Figure 1, a and b.) The cover of wetland perennials, however, was more strongly associated with seasonal (Nov-Jun) precipitation than with livestock grazing variables (Figure 1c). Precipitation data in Bovee et al. (2018) was not measured directly, but derived from the PRISM (Parameter-elevation Regressions on Independent Slopes) data set, an 800 m interpolation of weather gauge data in the United

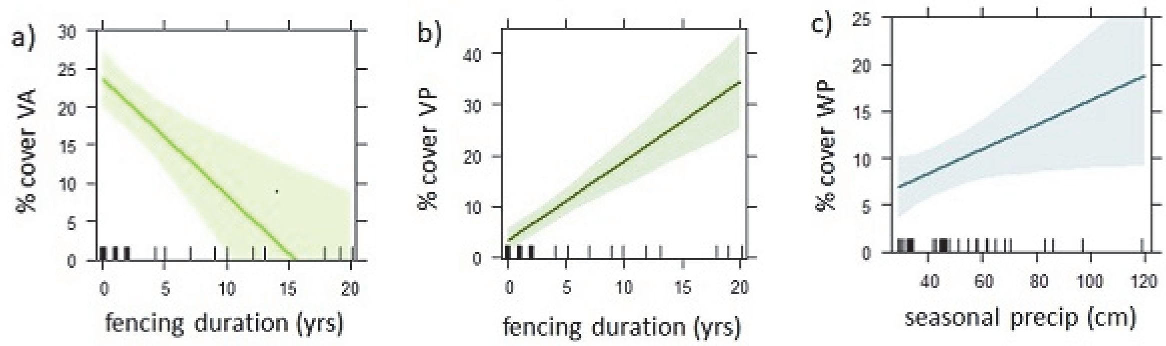


FIGURE 1**.** Linear relationships between the number of years a pool was fenced (fencing duration) and the cover of (a) vernal pool annuals (VA), (b) vernal pool perennials (VP); (c) relationship between seasonal precipitation and cover of wetland perennials (WP). Shading indicates confidence of fit (α < 0.05).

States that accounts for climatic variation associated with topography (Daly et al., 2008).

We have additionally asked how small-scale, short-term livestock use trends might lead to pool-scale, long-term differences in species composition in fenced versus unfenced vernal pools. We hypothesized that at small spatial scales, higher livestock use (as indicated by hoofprint cover and forage utilization) would be associated with higher cover of vernal pool perennials, signifying that livestock were drawn to areas containing species with higher forage value. We further hypothesized that this could, over time, explain shifts in vernal pool plant communities at larger spatial scales as livestock repeatedly targeted more palatable and robust vernal pool perennials.

### *Questions Asked in This Study*

Specifically, we asked the following questions:

1) Within-Year Grazing Effects: Where is livestock use concentrated within the vernal pools of the Modoc Plateau? Are differences in functional group cover associated with differences in livestock use at the 1-m$^2$ plot level?

2) Between-Year Grazing Effects: Are interannual changes in livestock use variables associated with interannual changes in functional group cover at the 1-m$^2$ plot level?

3) Long-Term, Pool-Scale Grazing Effects: Does species composition diverge in pools that have been fenced long-term? Do certain species emerge as indicators of long-term fenced or long-term unfenced pools?

## METHODS

To investigate questions about montane vernal pool plant communities and livestock grazing effects, we sampled plant species composition in 20 pools on the Modoc Plateau in northeastern California (Figure 2). Pools were selected because they contained *Orcuttia tenuis*, the subject of associated research. All pools were historically open to livestock grazing, and so grazing represented the baseline condition. Five of these 20 vernal pools had been fenced as early as 1991 with the intention of excluding livestock from *Orcuttia tenuis* occurrences. Fifteen pools were unfenced at the initiation of the study in 2009, with variation in the season of grazing among pools (see Appendix 1 for

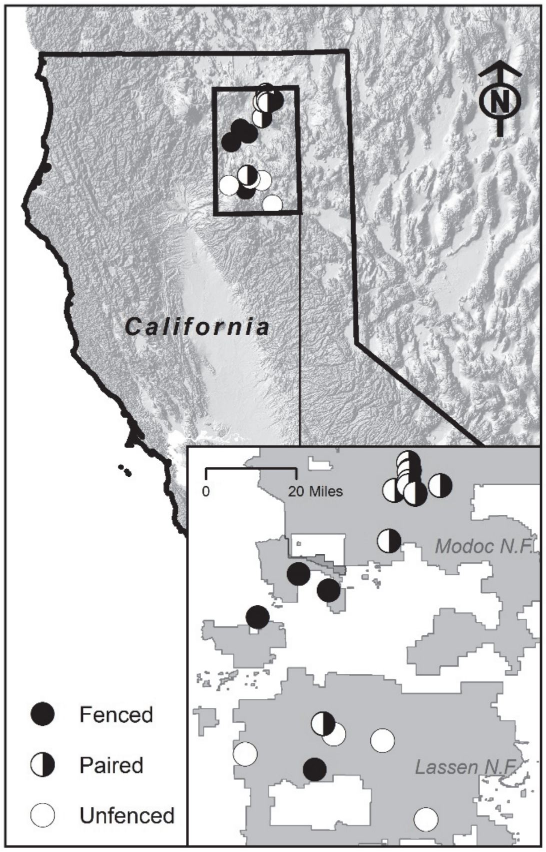


FIGURE 2. Location of study sites (Bovee et al., 2018).

more detail on study sites). Temporary livestock exclosures were constructed in summer 2009 to create paired grazed/ungrazed areas within 11 pools. In 2009 we established two 350-m$^2$ macroplots at each of the 11 pools with temporary fencing (one within the fenced exclosure, one outside), and one macroplot at each of the other sites. In all, 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, spanning 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 (and 1085 1-m$^2$ plots across the 31 macroplots in the study). To minimize edge effects, all plots were located more than 2 m from fences. Plant species were identified in each 1-m$^2$ plot and a visual estimation was made of percentage cover for each species, as well as hoofprints, bare ground and litter according to modified Daubenmire cover classes (Daubenmire, 1959). We used the Landscape Appearance Method to provide a qualitative assessment of forage utilization within plots following protocols established by the Bureau of Land Management (USDI, BLM, 1999). Nomenclature of identified plant species followed Baldwin et al. (2012).

We categorized species as either vernal pool specialists, wetland generalists, or upland generalists using distribution information from The Jepson Manual (Baldwin et al., 2012), as well as information on vernal pool species in Barbour et al. (2007) and Keeler-Wolf et al. (1998). Livestock grazing literature has long emphasized differential effects to annual versus perennial species (Díaz et al., 2007), and so we further distinguished functional groups by life span (annual versus perennial). See Appendix 2 for a list of species and functional groups. Descriptive statistics are presented to highlight broad differences in functional group composition between pools that had been grazed for >5 years and unfenced pools.

### *Within-year Grazing Trends (1-m$^2$ scale)*

To describe within-year livestock grazing trends, we tested the relationships between forage utilization, hoofprint cover, and functional group cover with linear mixed effects models (LMMs) using plot-scale (1-m$^2$) data. Linear mixed effects models were fit in R (R Core Team, 2019) using the lme4 package (Bates et al., 2015; Bolker et al., 2009). Forage utilization was classified as high where the class interval was > 40% (rangeland covered uniformly, less than 25% of current seed stalks remain intact), and low where < 40% (rangeland grazed lightly or in patches, most current seed stalks intact) and considered as a categorical variable (USDI, BLM, 1999). Hoofprint cover and functional group cover were included as continuous variables. We included plot nested within macroplot as a random effect to account for the repeated measures of pools that were visited in multiple years.

### *Between-year Grazing Trends (1-m$^2$ scale)*

To describe how interannual change in functional groups might vary with interannual change in livestock grazing use, we looked at the subsets of plots that were visited in more than one year for which the variables of interest (forage utilization, hoofprint cover, bare ground cover, litter cover) showed positive or negative change from year to year. These data were normally distributed, and ANOVA was applied to examine interannual changes in functional group cover for these variables. To further describe which interannual changes had the greatest impact on functional group cover, we created models with all possible combinations of fixed effect variables using a maximum likelihood estimation method. We then compared models using the AIC value, selecting the model with the lowest AIC value as the "best-fit" model. The best-fit models were then tested with LMMs, incorporating a plot identifier as a random effect to account for repeated measures of some plots. These models were fit in R (R Core Team, 2019) using the lme4 package (Bates et al., 2015; Bolker et al., 2009).

### *Long-term Grazing Trends (350-m$^2$ scale)*

We used nonmetric multidimensional scaling (NMDS), permutational analysis of variance, and indicator species analysis to examine the long-term effects of fencing on species composition at the macroplot scale. NMDS of Bray-Curtis distances between macroplots, based upon the relative average abundance of species, was used to visualize differences in species composition by fencing status. The Bray-Curtis dissimilarity metric in NMDS was selected because it weights abundant species over species that occur infrequently (Bray and Curtis, 1957; Minchin, 1987). Species cover values were averaged by macroplot, and included only if species occurred in greater than 5% of macroplots (n = 51 species). Heterogeneity of community structure by fencing status was assessed by first testing the homogeneity of dispersion to determine the degree of multivariate dispersion within each group and evaluate the appropriateness of PERMANOVA analysis with consideration for the unbalanced dataset (n = 24 macroplots fenced ≤ 5 years, n = 8 macroplots fenced > 5 years, n = 38 macroplots unfenced). Within-group and between-group differences in species composition were then compared using permutational analysis of variance (PERMANOVA) models of Bray-Curtis dissimilarities (Anderson, 2001). NMDS and PERMANOVA analyses were conducted using the vegan package (Oksanen et al., 2018) in R Version 3.5.1 (R Core Team, 2019).

We investigated the ecological preferences of species for fencing status categories with a correlation index (Dufrêne and Legendre, 1997). We used the indicspecies package (De Caceres, 2013) to calculate the association between species and fencing status using Pearson's phi coefficient of association (Chytrý et al., 2002), and derived indicators by fencing category and all possible combinations of fencing categories. We applied a correction on the phi coefficient to account for an unequal number of long-term fenced and long-termed unfenced pools (Tichý and Chytrý, 2006). We calculated point-biserial coefficients for on species abundance data averaged within year and within macroplot to determine indicator species for each fencing status category and combination of fencing status categories.

## RESULTS

Vegetation sampling in Modoc pools confirmed that these pools lack the invasive annual grass component dominant in lower elevation pools. Pools were found to contain a mix of vernal pool specialists and wetland generalists, with a very minor component of upland plants.

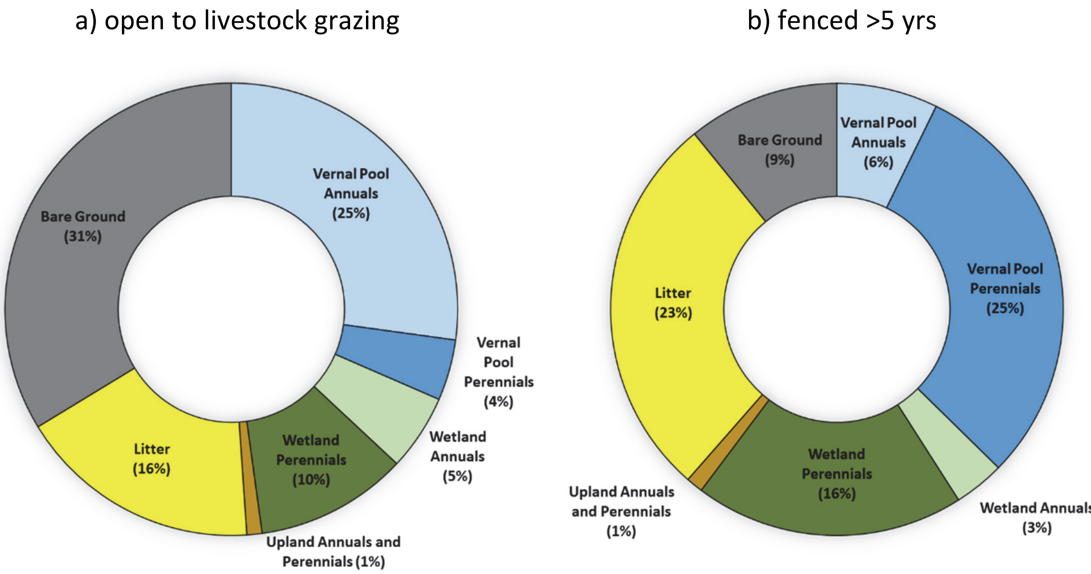


FIGURE 3. Average functional group composition for vernal pools within the study area in pools that were (a) open to livestock grazing (b) fenced for more than five years.

Mean cover of these functional groups differed dramatically between pools that were fenced for five or more years relative to unfenced pools (Figure 3, a and b). On average, cover of vernal pool annuals was four times higher in pools that were open to grazing ($x_{unfenced} = 24\%$, $x_{fenced >5 yrs} = 6\%$, $p < 0.01$), while cover of vernal pool perennials was over six times higher in pools that had been fenced for more than five years ($x_{unfenced} = 3\%$, $x_{fenced >5 yrs} = 25\%$, $p < 0.0001$). Bare ground cover was over three times higher in grazed pools years ($x_{unfenced} = 31\%$, $x_{fenced >5 yrs} = 9\%$, $p < 0.001$), and mean cover of perennial wetland generalists and litter was also higher in long-term fenced pools though not significantly so. Upland species (including invasives) were a negligible component of both grazed and fenced pools.

### *Within-year Grazing Trends (1-m² scale)*

At a small (1-m²) spatial scale, cover of vernal pool perennials was positively associated with high forage utilization ($\beta = 1.8$, $F_{1,2622} = 41.7$, $p < 0.0001$) (Figure 4) and, to a lesser degree, with hoofprint cover ($\beta = 0.15$, $F_{1,2622} = 41.6$, $p < 0.0001$) (Figure 5b). In plots where forage utilization was high, mean cover of vernal pool perennials was over twice that of plots where forage utilization was low (13% cover versus 6% cover) (Figure 4). The converse was found for vernal pool annuals. This functional group was negatively associated with high forage utilization ($\beta = -3.7$, $F_{1,2622} = 28.1$, $p < 0.0001$) and to a lesser degree, with hoofprint cover ($-0.28$, $F_{1,2622} = 22.0$, $p < 0.0001$, Figures 4 and 5a). Mean cover of vernal pool annuals was 60% lower in plots where forage utilization was low (21% cover versus 13% cover) (Figure 4). Relationships between cover of perennial wetland generalists, forage utilization, and hoofprint cover were not significant.

### *Between-year Grazing Trends (1-m² scale)*

There was much higher variance in the interannual change in the cover of vernal pool annuals from year to year ($\sigma^2 = 804$) relative to cover of vernal pool perennials ($\sigma^2 = 68$) or wetland perennials ($\sigma^2 = 181$). Of these three functional groups, interannual change in the cover of vernal pool annuals was most strongly associated with interannual change in grazing variables. Change in the cover of vernal pool annuals was

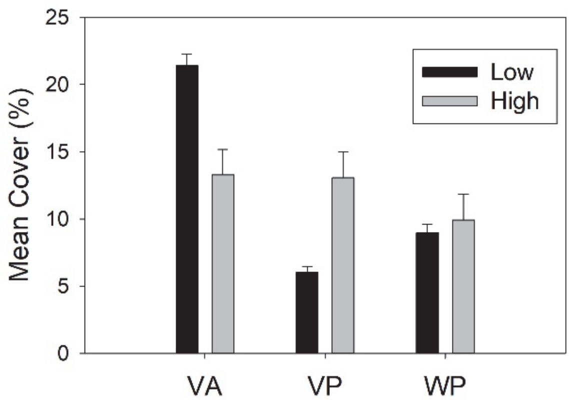


FIGURE 4. Mean cover (%) of vernal pool annuals (VA), vernal pool perennials (VP), and wetland perennials (WP) by forage utilization category (Low, High) at the 1-m$^2$ plot scale. Bars indicate 95% C.I.

negatively associated with increases in bare ground cover, increases in litter cover, and increases in forage utilization (Table 1).

These relationships were not as strong for perennial functional groups. Change in the cover of vernal pool perennials had a weak negative relationship with changes in litter cover, while increased forage utilization from year to year was negatively associated with the cover of wetland perennials (Figure 6). On average, plots that experienced an increase in bare ground cover from year to year averaged a six-fold loss in cover of vernal pool annuals relative to plots that experienced a decrease in bare ground cover (-2% cover versus -12% cover, Figure 6b), and plots where forage utilization increased averaged a 9% decrease in cover relative to a 2% increase in cover where forage utilization decreased (Figure 6a). In addition, litter increases were associated with larger losses of vernal pool annuals relative to litter decreases (-9% versus -6%) (Figure 6d). These relationships were sometimes significant but weak for vernal pool perennials and wetland perennials. The exception was a decrease in the cover of wetland perennials with increased forage utilization (Figure 6a).

### *Long-term Grazing Trends (350-m$^2$ scale)*

Separation of plant species composition by fencing status was visualized with a plot of the first two axes of NMDS ordination (Figure 7). Fencing status was a significant contributor to differences in plant community composition between macroplots ($F_{PERMANOVA} = 3.94$, $R^2 = 0.11$, $p < 0.01$). While between-group species composition was significantly different for long-term fenced macroplots and both unfenced macroplots ($F_{PERMANOVA} = 5.41$, $R^2 = 0.11$, $p < 0.01$) and short-term fenced plots ($F_{PERMANOVA} = 6.76$, $R^2 = 0.18$, $p < 0.01$) relative to within-group species composition, this relationship was not significant between unfenced macroplots and short-term fenced macroplots ($F_{PERMANOVA} = 1.38$, $R^2 = 0.02$, $p = 0.53$).

### *Indicator Species*

A broad range of species emerged as indicators of pools fenced for more than five years (Table 2). The strongest indicator was the vernal pool perennial *Eryngium mathiasiae* ($r^{\Phi}{}_{g} = 0.64$, $p < 0.01$), followed by the wetland perennial *Eleocharis macrostachya* ($r^{\Phi}{}_{g} = 0.57$, $p < 0.01$). No species emerged as indicators for unfenced versus short-term fenced pools, indicating a large degree of overlap in species composition between these two groups. However, four species were significantly correlated with the combination of those fencing categories as contrasted with long-term fenced pools. Of these, three were vernal pool annuals (*Gratiola heterosepala*, *Navarretia intertexta*, *Castilleja campestris*).

## DISCUSSION

At small spatial scales, livestock use was positively associated with the cover of vernal pool perennials, suggesting that livestock may be drawn to patches of vegetation within pools

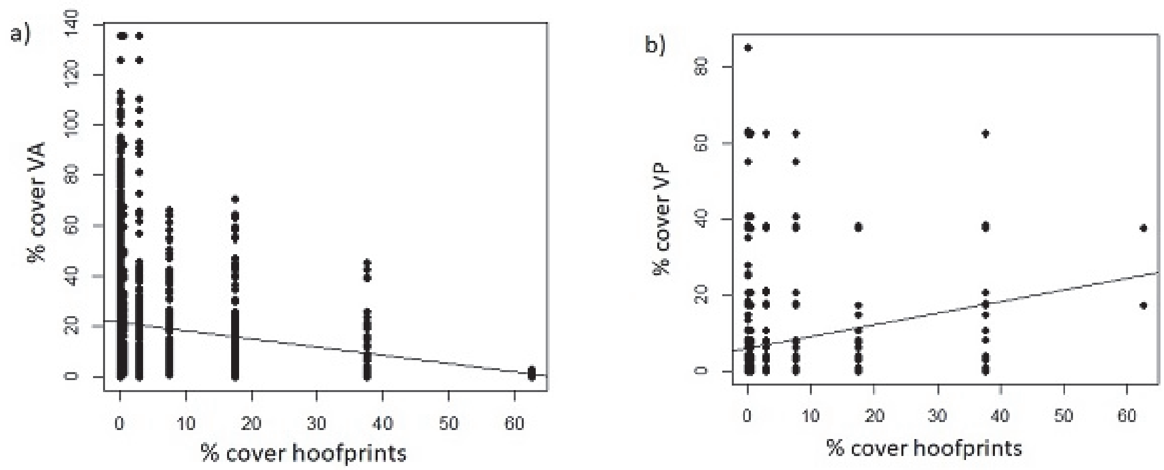


FIGURE 5. Relationship between hoofprint cover at the 1-m$^2$ plot scale and (a) cover of vernal pool annuals (VA), (b) vernal pool perennials (VP).

TABLE 1. Best fit mixed effect linear model results, with interannual change (Δ) in livestock variables as fixed effects predicting interannual change (Δ) in functional group cover.

| Δ Cover | Esti-mate | SE | $F_{df}$ | P | Model $R^2$ |
|---|---|---|---|---|---|
| **Vernal Pool Annuals** | | | | | 0.63 |
| Δ Bare Ground | -0.32 | 0.02 | $227.22_{1,1908}$ | <0.0001 | |
| Δ Forage Utilization | -0.22 | 0.04 | $36.34_{1,1812}$ | <0.0001 | |
| Δ Litter | -0.14 | 0.02 | $45.09_{1,1545}$ | <0.0001 | |
| **Vernal Pool Perennials** | | | | | 0.33 |
| Δ Litter | -0.01 | 0.01 | $1.94_{1,1678}$ | 0.16 | |
| **Wetland Perennials** | | | | | 0.33 |
| Δ Forage Utilization | -0.10 | 0.02 | $27.81_{1,1626}$ | <0.0001 | |

that contain these species. Plots with high forage utilization had twice the cover of vernal pool perennials, and hoofprint cover was also positively associated with vernal pool perennials (Figures 4 and 5**)** The converse trend was observed for vernal pool annuals. Plots with high forage utilization had 60% less cover of vernal pool annuals relative to plots with low forage utilization, and hoofprint cover decreased with increased cover of vernal pool annuals. Vernal pool annuals are mostly diminutive in stature, and some (like *Orcuttia tenuis*) produce an exudate that may deter herbivory (Reeder, 1982; Keeley, 1998). Forage utilization and hoofprint cover were not significantly associated with the cover of wetland perennials, suggesting that species such as *Eleocharis macrostachya*, the most abundant species in this functional group, may not be preferred by livestock in the Modoc Plateau pools.

Although livestock may be drawn to areas with high cover of vernal pool perennials, livestock grazing effects to this functional group were not apparent over the short-term. Variation in forage utilization was, however, significantly

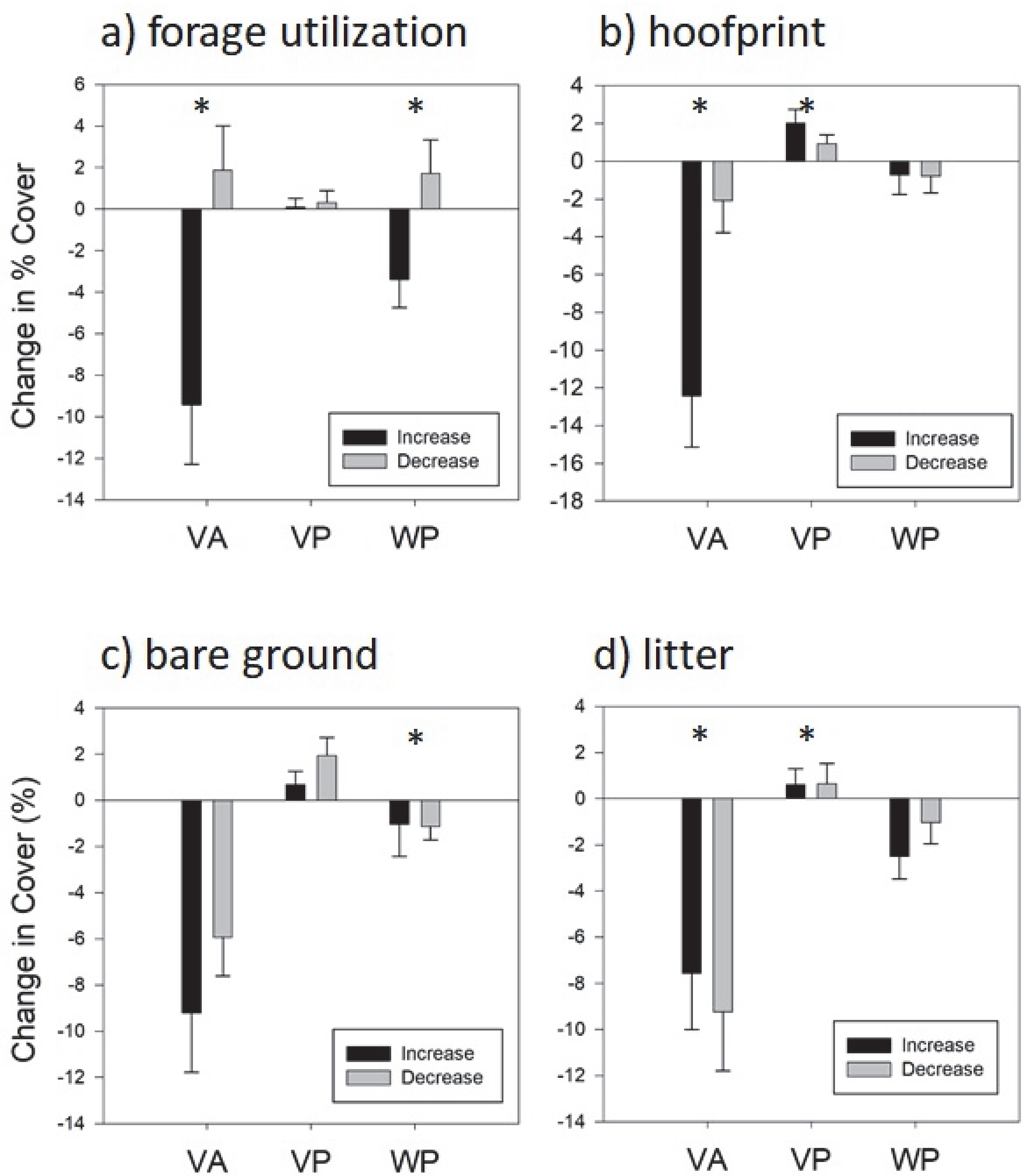


FIGURE 6. Interannual change (% cover) of vernal pool annuals (VA), vernal pool perennials (VP), and wetland perennials (WP) by interannual change (increase or decrease) in a) forage utilization, b) hoofprint cover, c) bare ground cover, and d) litter cover. Asterisks indicate difference significant at $\alpha = 0.05$.

associated with variation in the cover of wetland perennials (Figure 6a), suggesting that increased livestock use can decrease the cover of this functional group over short time frames. Overall, year to year variation in the cover of vernal pool perennials and wetland perennials across the three-year study was low.

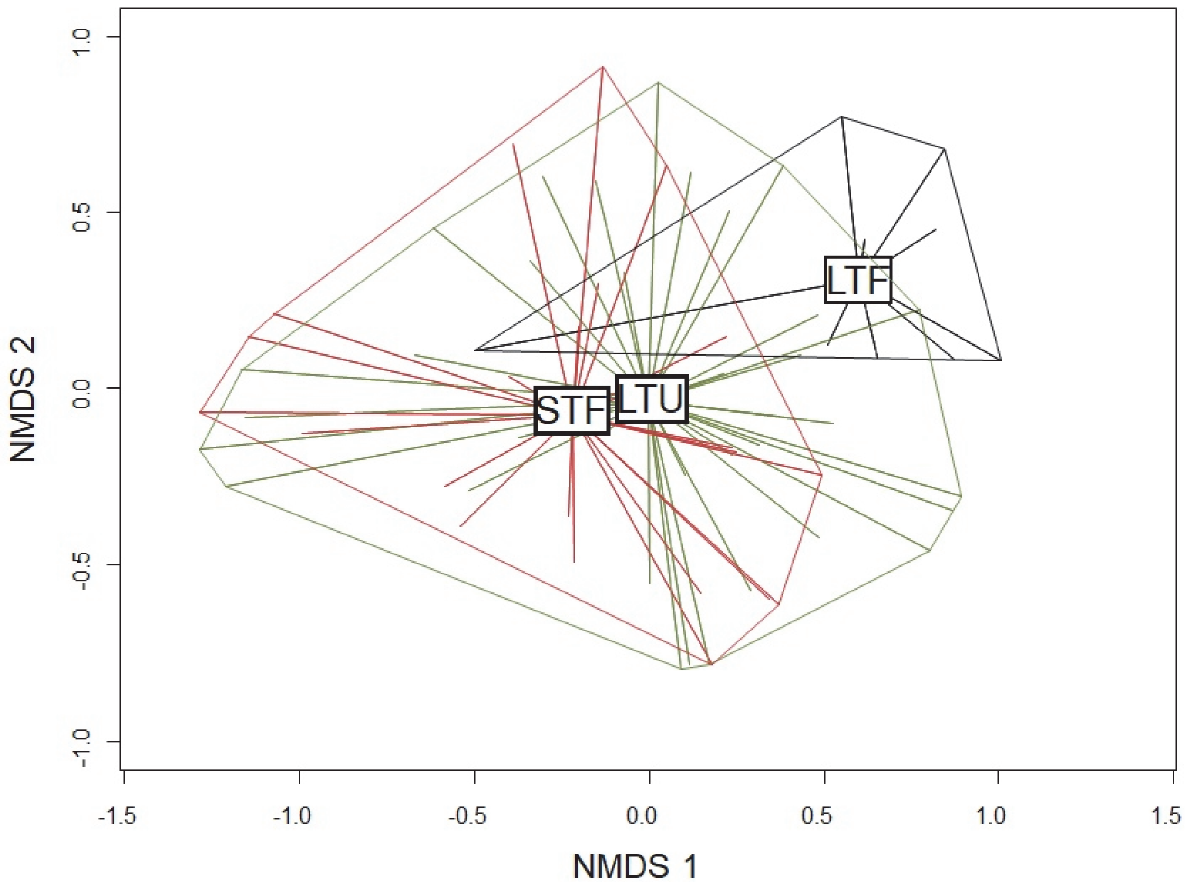


FIGURE 7. NMDS ordination of species composition by macroplot based upon Bray-Curtis dissimilarity and displayed by group (LTF = fenced > 5 years, STF = fenced ≤ 5 years, LTU = unfenced) with label displayed at group centroid, and vectors showing macroplot distance to group centroid. NMDS Stress = 0.18, k = 3 with Axis 1 and Axis 2 displayed below.

Short-term livestock grazing effects to vernal pool annuals were more apparent. Results suggest complexity in the relationship between livestock grazing and vernal pool annuals, with both positive and negative short-term effects. This is consistent with findings in Merriam et al. (2016), which focused specifically on the vernal pool annual grass *Orcuttia tenuis*. Interannual change in the cover of vernal pool annuals was strongly and significantly associated with several livestock use variables (bare ground cover, forage utilization, and litter) (Figure 6a, b, and d**)**. Where bare ground increased from year to year, cover of vernal pool annuals decreased. Interestingly, increases in litter cover were also associated with decreased cover of this functional group. It appears that vernal pool annuals can be negatively impacted by grazing where it results in increased bare soil (perhaps indicating soil disturbance or displacement, particularly when soils are wet) but can also benefit from year-to-year reductions in litter cover. Faist and Beals (2018) found that the addition of just one centimeter of litter significantly altered plant community structure in restored vernal pools in the Central Valley. This suggests the potential for grazing management to optimize the beneficial effects of grazing if livestock can be introduced later in the season when soils have dried and the potential for soil displacement decreases.

TABLE 2. Indicator species with significant correlations with fencing status groups at $p < 0.05$. $r^{\Phi}_{g}$ = Pearson's phi coefficient of association.

| Species | Functional Group | $r^{\Phi}_{g}$ | p-value |
|---|---|---|---|
| **Fenced > 5 years** | | | |
| *Eryngium mathiasiae* | VP | 0.64 | <0.01 |
| *Eleocharis macrostachya* | WP | 0.57 | <0.01 |
| *Epilobium cleistogamum* | VA | 0.39 | <0.05 |
| *Epilobium densiflorum* | WA | 0.38 | <0.01 |
| *Madia glomerata* | UA | 0.29 | <0.05 |
| *Veronica peregrina* | WA | 0.28 | <0.05 |
| *Isoëtes howellii* | VP | 0.28 | <0.05 |
| **Unfenced + Fenced ≤ 5 years** | | | |
| *Gratiola heterosepala* | VA | 0.42 | <0.01 |
| *Navarretia intertexta* | VA | 0.39 | <0.01 |
| *Muhlenbergia richardsonis* | VP | 0.37 | <0.05 |
| *Castilleja campestris* | VA | 0.33 | <0.05 |

This study also highlights the importance of considering fencing effects over longer time scales than the length of most research. While five pools had a long ( > 5-year) history of livestock exclusion, the temporary fencing exclosures established for the study were sampled only two years post-fencing. This short time frame was insufficient to detect the divergence in functional group composition observed after longer fencing durations. Over the short-term (e.g., five or fewer years of fencing), species composition was not significantly different in fenced versus unfenced macroplots. Macroplots fenced for more than five years, however, were characterized by a distinct plant community, with perennial species such as *Eryngium mathisiae* emerging as indicators of fencing. High cover of vernal pool perennials in long-term exclosures suggests that their abundance prior to the advent of livestock grazing may have been dramatically higher than what is currently observed in unfenced or short-term fenced pools. Although biomass was not measured directly, the high elevation, short growing season, and lack of invasive species in the pools of the Modoc Plateau may all contribute to a slower accumulation of litter or thatch relative to the pools of the Central Valley, and explain why no significant differences in litter cover were observed after the short-term fencing experiment.

Our results suggest that over time, excluding livestock from vernal pools may lead to decreased cover of vernal pool annuals, the very suite of species that land managers often prioritize for conservation due to their endemism and rarity. However, leaving pools open to livestock grazing can result in decreased cover of vernal pool perennials. Because nearly all pools on the Modoc Plateau were open to grazing over the past century, we have no true reference condition to assess the historical distribution of vernal pool perennials. This functional group may be underrepresented on the landscape relative to pre-livestock grazing levels. Although our results showed short-term, small-scale decreases in wetland perennials with increased forage utilization, over the long-term grazing effects were not significant for this group. Cover of wetland perennials was more strongly related to seasonal precipitation, and highly variable between pools (see Bovee et al., 2018).

Although invasives are not currently a concern in many Modoc pools, projected warmer winters predicted under some climate change scenarios may result in increased evapotranspiration, diminished snowpack, and earlier pool drying in spring and summer months (Cayan et al., 2008; Berghuijs et al., 2014). These changes may create more favorable conditions for invasive species. *Elymus caput-medusae* (medusahead) and *Ventenata dubia* (North Africa grass) are both invasive species known to occur adjacent to the pools of the Modoc Plateau. Earlier drying of pools may allow invasive species such as these to invade habitat previously too wet for them to tolerate (Gosejohan et al., 2017).

While this study took a detailed look at vegetative composition and small-scale environmental conditions, it did not measure factors such as pool depth and hydroperiod that would also contribute strongly to the vegetative composition of each pool (see Gosejohan et al., 2017, Merriam et al., 2019). Direct measurement of hydrologic variables would provide a more complete picture of the environmental influences on plant community structure and how they may interact with livestock grazing variables.

### *Management Recommendations*

Negative short-term, small-scale relationships between livestock grazing variables and vernal pool annuals are usually outweighed by the longer-term benefits of livestock grazing to this functional group. Overall, livestock grazing at the intensity and timing observed in this study was of long-term benefit to vernal pool annuals, including the rare species *Orcuttia tenuis.* However, if grazing were to increase in intensity or duration in unfenced pools, short-term impacts may be amplified, and we may see long-term benefits unable to surmount short-term negative effects.

These findings lead us to question what disturbance vectors may have periodically reduced litter and biomass prior to the advent of livestock grazing. Native herbivores (mule deer, pronghorn antelope, elk, small mammals) may contribute to variation in vegetative biomass and litter within pools, and current versus historical levels of use in vernal pools are unknown. Fire may have played a larger role historically in reducing litter accumulations by periodically burning through vernal pools. While grazed pools in our study averaged 30% bare ground cover and would be unlikely to carry fire, long-term fenced pools averaged 9% bare ground, with a more continuous fuel bed that could carry late-season fire. Assessment of prescribed fire as a management tool in montane vernal pools could help us to determine whether late-season fire could be used as a management tool in ungrazed pools to set back litter accumulation.

Should pools that are currently fenced be reopened to grazing? Fencing was usually constructed in response to heavy livestock impacts within those pools, and removal of fencing has the potential to cause a return to these adverse conditions. Timing and intensity of grazing should be taken into account when evaluating the reintroduction of livestock grazing to fenced pools. Opening pools to livestock grazing late in the season and perhaps not in every year may maximize beneficial effects to vernal pool annuals while also maintaining cover of vernal pool perennials. Livestock grazing management should be adaptive in nature, and adjusted if monitoring indicates that season of use or high hoofprint cover is resulting in excessive soil displacement. Future work will evaluate fenced pools to determine whether they might benefit from late-season livestock grazing in some years, and establish litter thresholds at which this should be considered.

## Literature Cited


Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32-46.

Baldwin, B.G., D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken. 2012. The Jepson Manual: Vascular Plants of California. University of California Press, Berkeley, CA.

Barbour, M.G., A. Solomeshch, and J.J. Buck. 2007. Classification, Ecological Characterization, and Presence of Listed Plant Taxa of Vernal Pool Associations in California. United States Fish and Wildlife Service Agreement/Study Number 814205 G238, University of California, Davis, CA.

Bates, D., M. Maechler, B. Bolker and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Berghuijs, W. R., R.A. Woods, and M. Hrachowitz. 2014. A precipitation shift from snow towards rain leads to a decrease in streamflow. Nature Climate Change 4(7): 583.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S.S.White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127-135.

Bovee, K. M., K.E. Merriam, and M.C. Gosejohan. 2018. Livestock grazing affects vernal pool specialists more than habitat generalists in montane vernal pools. Applied Vegetation Science 21(1): 12-20.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349.

Cayan, D. R., E.P. Maurer, M.D. Dettinger, and K. Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change 87:21-42.

Chytrý, M., L., Tichý, J. Holt, and Z. Botta-Dukát. 2002. Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13:79-90.

Cingolani, A. M., I. Noy-Meir, and S. Díaz. 2005. Grazing effects on rangeland diversity: A synthesis of contemporary models. Ecological Applications 15:757-773.

Daly, C., M. Halbleib, J.I. Smith, W.P. Gibson, M.K. Doggett, G.H. Taylor, J. Curtis, and P.P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology: A Journal of the Royal Meteorological Society 28:2031-2064.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-64.

De Cáceres, M. 2013. How to use the indicspecies package (ver. 1.7. 1). R Project: 29.

Díaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D.G. Milchunas, C. Skarpe, G. Rusch, M. Sternberg, I. Noy-Meir, J. Landsberg, W. Zhang, H. Clark, and B.D. Campbell. 2007. Plant trait responses to grazing—a global synthesis. Global Change Biology 13:313-341.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Faist, A. M., and S.C. Beals. 2018. Invasive plant feedbacks promote alternative states in California vernal pools. Restoration Ecology 26: 255-263.

Gosejohan, M. C., P.J. Weisberg, and K.E. Merriam. 2017. Hydrologic influences on plant community structure in vernal pools of northeastern California. Wetlands 37:257-268.

Harrison, S., B.D. Inouye, and H.D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology 17:837-845.

KEELER-WOLF, T., D.R. ELAM, K. LEWIS, and S.A. FLINT. 1998. California vernal pool assessment preliminary report. In. State of California, Department of Fish and Game, Sacramento, CA.

KEELEY, J.E. 1998. Diel acid fluctuations in C4 amphibious grasses. Photosynthetica 35: 273-277.

KEELEY, J.E., and P.H. ZEDLER. 1998. Characterization and global distribution of vernal pools. Pages 1-14 in C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren, Jr., and R. Ornduff (Editors.), Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 conference California Native Plant Society, Sacramento, CA.

KRAUSMAN, P. R., D.E. NAUGLE, M.R. FRISINA, R. NORTHRUP, V.C. BLEICH, W.M. BLOCK, M.C. WALLACE, and J.D. WRIGHT. 2009. Livestock grazing, wildlife habitat, and rangeland values. Rangelands 31(5): 15-19.

MARTY, J.T. 2015. Loss of biodiversity and hydrologic function in seasonal wetlands persists over 10 years of livestock grazing removal. Restoration Ecology 23:548-554.

MERRIAM, K.E., M.C. GOSEJOHAN, P.J. WEISBERG, and K.M. BOVEE. 2016. Livestock use has mixed effects on slender Orcutt grass in northeastern California vernal pools. Rangeland Ecology & Management 69(3):85-194.

MERRIAM, K.E., M.C. GOSEJOHAN, and P.J. WEISBERG. 2019. The effects of hydroregime on vernal pool plant communities in northeastern California. Pages 45-59 in R. A. Schlising, E.E. Gottschalk Fisher, C.M. Guilliams, and B. Castro (Editors), Vernal Pool Landscapes: Past, Present and Future. Studies from the Herbarium Number 20, California State University, Chico, CA.

MILCHUNAS, D.G., and W.K. LAUENROTH. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

MINCHIN, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Theory and models in vegetation science. Springer, Dordrecht, The Netherlands.

NOY-MEIR, I., M. GUTMAN, and Y. KAPLAN. 1989. Responses of Mediterranean grassland plants to grazing and protection. The Journal of Ecology:290-310.

OKSANEN, J., F.G. BLANCHET, R. KINDT, P. LEGENDRE, P.R. MINCHIN, R.B. O'HARA, G.L. SIMPSON, P. SOLYMOS, M.H.H. STEVENS, and H. WAGNER. 2018. Package vegan: community ecology package version 2.3-1.

OLFF, H., and M.E. RITCHIE. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13:261-265.

PYKE, C.R., and J. MARTY. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. Conservation Biology 19:1619-1625.

R CORE TEAM. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

REEDER, J.R. 1982. Systematics of the tribe Orcuttieae (Gramineae) and the description of a new segregate genus, *Tuctoria*. American Journal of Botany 69:1082-1095.

SOLOMESHCH, A.I., M.G. BARBOUR, and R.F. HOLLAND. 2007. Vernal pools. Terrestrial Vegetation of California, 3rd Edition. University of California Press, Berkeley, CA

TICHÝ, L., and M. CHYTRÝ. 2006. Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17:809-818.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA, FS). 2018. Natural Resource Information System (NRIS): Threatened, endangered, and sensitive plant (TESP) – Invasive Species Geodatabase. Washington, DC. [Accessed 29 November 2018.]

U.S. DEPARTMENT OF THE INTERIOR, BUREAU OF LAND MANAGEMENT (USDI, BLM). 1999. Utilization Studies and Residual Measurements. Denver, CO.

APPENDIX 1. Vernal pool study sites, including site name, location, elevation (m), approximate pool size (ha), grazing status, year fenced, type of livestock, animal unit month (AUM), and season of grazing.

| Site Name | Location[1] | Elevation (m) | Pool Size (ha) | Grazing Status[2] | Year Fenced[3,6] | Livestock[6] | AUM[4, 6] | Season[5,6] |
|---|---|---|---|---|---|---|---|---|
| Adobe North | LNF | 1097 | 5 | Not grazed | 1991 | __ | __ | __ |
| Fort Mountain | LNF | 1035 | 2 | Not grazed | 2007 | __ | __[6] | __[6] |
| Grassy Lake | LNF | 1463 | 12 | Paired plots | __[6] | Cattle | 135 | Late |
| Green Place | BLM | 1038 | 11 | Not grazed | 2001 | __[6] | __[6] | __[6] |
| Hackamore North | MDF | 1426 | 56 | Paired plots | __[6] | Sheep | 1915-2471 | All |
| Hackamore South | MDF | 1427 | 56 | Paired plots | __[6] | Sheep | 1915-2471 | All |
| Henski | MDF | 1459 | 14 | Grazed | __[6] | Cattle | 116-304 | All |
| Highway 139 | MDF | 1493 | 20 | Paired plots | __[6] | Cattle | 110-250 | Late |
| Little Bunchgrass Meadow[7] | LNF | 1602 | 1 | Not grazed | 2004 | __[6] | __[6] | __[6] |
| McKay North | MDF | 1461 | 150 | Paired plots | __[6] | Cattle | 291-372 | Early |
| McKay South | MDF | 1462 | 150 | Paired plots | __[6] | Cattle | 291-372 | Early |
| Mud Lake | MDF | 1431 | 185 | Paired plots | __[6] | Cattle | __[8] | __[8] |
| Northeast Coyote Springs | LNF | 1521 | 4 | Paired plots | __[6] | Cattle | 345-413 | Early |
| Southeast Ebey Lake | LNF | 1706 | 158 | Grazed | __[6] | Cattle | 110-250 | Late |
| South Whalen | MDF | 1331 | 7 | Not grazed | 2009 | __[6] | 338-605 | __[6] |
| Spaulding | MDF | 1453 | 144 | Paired plots | __[6] | Cattle | 116-304 | All |
| Spaulding West | MDF | 1451 | 144 | Paired plots | __[6] | Cattle | 116-304 | All |
| Swain Mountain | LNF | 1767 | 6 | Grazed | __[6] | Cattle | 100-199 | Late |
| Tamarack Flat | LNF | 1645 | 30 | Grazed | __[6] | Cattle | 338-605 | Late |
| Whitney Reservoir | MDF | 1427 | 97 | Paired plots | __[6] | Sheep | 1915-2471 | 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 prior to the grazing season in 2010, except for Grassy Lake, where permanent paired plots were installed in 1997.

[4] AUM is shown as a range where values varied over the three years of our study. Sheep and cattle AUM are not directly comparable.

[5] Season of grazing is defined as: a) Early, with livestock removed prior to August, b) Late, with livestock released after July, and c) All season, where livestock remain on pastures throughout the season.

[6] ___. Type of livestock, AUM, and season of grazing is not applicable at ungrazed sites. Year is not applicable at grazed sites.

[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.

APPENDIX 2. Plant species identified within plots and functional group assignation.

| |
|---|
| Upland Annual (UA) |
| *Acmispon americanus* (Nutt.) Rydb. var. *americanus* |
| *Acmispon wrangelianus (*Fisch. & C.A. Mey.) D.D. Sokoloff |
| *Agoseris heterophylla* (Nutt.) Greene |
| *Apera interrupta* (L.) P. Beauv. |
| *Bromus arvensis* L. |
| *Bromus tectorum* L. |
| *Croton setiger* Hook. |
| *Elymus caput-medusae* L. |
| *Epilobium brachycarpum* C. Presl |
| *Hordeum marinum* Huds. ssp. *gussoneanum* (Parl.) Thell. |
| *Lactuca serriola* L. |
| *Lagophylla ramosissima* Nutt. |
| *Madia glomerata* Hook. |
| *Microsteris gracilis* (Hook.) Greene |
| *Mimulus bicolor* Benth. |
| *Mimulus torreyi* A. Gray |
| *Panicum capillare* L. |
| *Polygonum aviculare* ssp. *depressum* (Meisn.) Arcang. |
| *Polygonum douglasii* Greene |
| *Rigiopappus leptocladus* A. Gray |
| *Tragopogon dubius* Scop. |
| *Trichostema oblongum* Benth. |
| Upland Perennial (UP) |
| *Artemisia arbuscula* Nutt. |
| *Artemisia cana* Pursh |
| *Artemisia tridentata* Nutt. |
| *Carex athrostachya* Olney |
| *Cuscuta californica* Hook. & Arn. var. *papillosa* Yunck. |
| *Danthonia unispicata* (Thurb.) Munro ex Vasey |
| *Elymus elymoides* (Raf.) Swezey |
| *Grindelia nana* Nutt. |
| *Lomatium macrocarpum* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose |
| *Muhlenbergia richardsonis* (Trin.) Rydb. |
| *Pinus ponderosa* Douglas ex Lawson & C. Lawson |
| *Poa bulbosa* L. |
| *Poa secunda* J. Presl |
| *Toxicoscordion venenosum* (S. Watson) Rydb. var. *venenosum* |
| Vernal Pool Annual (VA) |
| *Alopecurus saccatus* Vasey |
| *Castilleja campestris* (Benth.) T.I. Chuang & Heckard ssp. *campestris* |
| *Downingia bicornuta* A. Gray |
| *Epilobium cleistogamum* (Curran) Hoch & P.H. Raven |

APPENDIX 2 continued.

| |
|---|
| Vernal Pool Annual (VA), continued |
| *Euphorbia serpyllifolia* Pers. |
| *Gnaphalium palustre* Nutt. |
| *Gratiola heterosepala* H. Mason & Bacig. |
| *Juncus hemiendytus* F.J. Herm. |
| *Mimulus tricolor* Lindl. |
| *Montia linearis* (Hook.) Greene |
| *Muhlenbergia filiformis* (Thurb. ex S. Watson) Rydb. |
| *Navarretia intertexta* (Benth.) Hook. |
| *Orcuttia tenuis* Hitchc. |
| *Plagiobothrys bracteatus* (Howell) I.M. Johnst. |
| *Plagiobothrys cognatus* (Greene) I.M. Johnst. |
| *Polygonum polygaloides* Meisn. |
| *Porterella carnosula* (Hook. & Arn.) Torr. |
| *Psilocarphus brevissimus* Nutt. |
| *Tuctoria greenei* (Vasey) Reeder |
| Vernal Pool Perennial (VP) |
| *Brodiaea coronaria* (Salisb.) Engl. |
| *Damasonium californicum* Torr. ex Benth. |
| *Eryngium articulatum* Hook. |
| *Eryngium mathiasiae* M.Y. Sheikh |
| *Isoetes howellii* Engelm. |
| *Pilularia americana* A. Braun |
| *Plagiobothrys mollis* (A. Gray) I.M. Johnst. |
| *Pyrrocoma racemosa* (Nutt.) Torr. & A. Gray |
| Wetland Annual (WA) |
| *Cyperus squarrosus* L. |
| *Deschampsia danthonioides* (Trin.) Munro |
| *Eleocharis bella* (Piper) Svenson |
| *Epilobium densiflorum* (Lindl.) Hoch. & P.H. Raven |
| *Juncus bufonius* L. var. *occidentalis* F.J. Herm. |
| *Myosurus minimus* L. |
| *Rorippa curvisiliqua* (Hook.) Besser ex Britton |
| *Veronica peregrina* L. ssp. *xalapensis* (Kunth) Pennell |
| Wetland Perennial (WP) |
| *Alopecurus geniculatus* L. |
| *Eleocharis macrostachya* Britton |
| *Juncus mexicanus* Willd. |
| *Juncus nevadensis* S. Watson |
| *Juncus tenuis* Willd. |
| *Marsilea oligospora* Goodd. |
| *Ranunculus aquatilis* L. |