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# Cattle waste reduces plant diversity in vernal pool mesocosms

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## ABSTRACT

In California, much of the remaining vernal pool habitat is used for cattle grazing. Some studies suggest that grazing helps promote native plant diversity on grasslands, but the impact of grazing on plants that reside in pool basins is largely unknown. We investigated how one aspect of cattle grazing, the deposition of waste, affects these plant species by adding dung and urine to mesocosms lined with vernal pool soil. As a result of dung input, orthophosphate, conductivity, and turbidity increased in our mesocosms while dissolved oxygen decreased. Such changes in water quality are consistent with a shift toward a eutrophic state. Algal biomass and percent-cover also increased in dung-treated mesocosms. When the mesocosms dried, vascular plant species richness and percent-cover in dung-treated mesocosms were reduced by up to 54% and 87%, respectively. We attribute this to light attenuation by algal mats that flourished in the nutrient-enriched water. We also found that dung input caused significant, but weak, shifts in the composition of the vascular plant community. We conclude that cattle grazing may be detrimental to plant communities in vernal pools via increased nutrient loading, which promotes algal growth. Any beneficial effects of grazing may thus be limited to the surrounding grassland. Studies that examine the regional-scale impacts of grazing on vernal pool grasslands should separately consider the impacts to local-scale (i.e., within-pool) plant diversity, as most of the threatened and endangered plant species of California vernal pools reside primarily in pool basins.

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## 1. Introduction

Temporary ponds found in Mediterranean climate regions are generally known as vernal pools. Such pools inhabit shallow depressions that have an underlying impermeable substrate (Holland and Jain, 1981), which supports a perched water table in the rainy season. Vernal pools are typically filled with rainwater during winter and spring and are desiccated during summer and fall. These cycles result in distinct aquatic and terrestrial communities in pool basins at different times of year (Williams, 1996). Worldwide, vernal pools are a focus of conservation efforts due to their high levels of species endemism and declining numbers (Ruiz, 2008; Serrano and Zunzunegui, 2008; Zacharias and Zamparas, 2010). Vernal pools in California, for example, contain over 60 endemic plant and animal taxa (Holland and Jain, 1981; King et al., 1996), and many of these are listed as threatened or endangered (Federal Register, 2003). Furthermore, only 3-10% of the historic expanse of vernal pool habitat in California remains due to agriculture and urbanization (Holland, 1978; Keeley and Zedler, 1998).

Many of the remaining pools in California exist on grasslands used for cattle grazing (hereafter referred to simply as grazing). Although grazing is a point of contention in California vernal pool (CVP) management, it is generally believed that management strategies should include at least some grazing (Vollmar, 2002; Federal Register, 2003; Marty, 2005). This view stems largely from empirical studies indicating that properly managed grazing can play a role in promoting native plant diversity (species richness and/or cover) on grasslands at the regional scale (Bokdam and Gleichman, 2000; Towne et al., 2005; Brudvig et al., 2007; but see Kimball and Schiffman, 2003). This conclusion appears to hold for grasslands containing vernal pools (Marty, 2005). On such grasslands, however, it is important to distinguish between the effects of grazing on plant diversity at the regional-scale (i.e., pools and the surrounding grassland matrix) versus at the local-scale (i.e., pool basins only) and to contrast the pool habitat from the surrounding grassland. Most of the threatened and endangered plants found in CVPs reside primarily in pool basins rather than in the surrounding grassland (Federal Register, 2003; Barbour et al., 2007). Studies have largely overlooked the impact of grazing on these species at the local scale. The few studies that have included such species suggest that grazing is at best neutral to native plant diversity in pool basins, regardless of the effects on diversity at the regional scale (Marty, 2005; Bouahim et al., 2010). This possible scale dependency illustrates the need for grazing studies targeting the plants that grow in pool basins.

One aspect of grazing that may be detrimental to plants in pool basins is the deposition of dung and urine. These waste products



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can enter vernal pools directly when cattle excrete while standing in pool basins (R. Croel and J. Kneitel, personal observations and unpublished data) or indirectly through runoff from adjacent land (Carpenter et al., 1998). Cattle waste poses a well-known threat to watershed drainages, shallow lakes, and ponds by fostering eutrophic conditions, which can stimulate algal blooms (Carpenter et al., 1998; Belsky et al., 1999; Smith et al., 1999; Anderson et al., 2002). In shallow water bodies, algal blooms can occlude light from the macrophyte "understory," resulting in macrophyte loss and an overall reduction in ecosystem functioning (Smith et al., 1999; Smith and Schindler, 2009). It stands to reason that plants in CVPs may be similarly threatened by cattle waste. Potentially compounding this threat is that the deposition of dung and urine is non-random at the landscape scale (Wallis de Vries and Schippers, 1994; James et al., 2007). Cattle have a tendency to congregate near sources of water (Wallis de Vries and Schippers, 1994; Belsky et al., 1999; Schomberg et al., 2000; James et al., 2007), which could result in higher levels of waste deposition in and immediately adjacent to vernal pools.

The phenologies of the plants residing in pool basins are strongly tied to the seasonality of vernal pools, which can be divided into three phases: an "aquatic phase," a "terrestrial phase," and a "drought phase" (Wiggins et al., 1980; Zedler, 1987; Williams, 1996; Keeley and Zedler, 1998). These phases are typical of vernal pools worldwide (Keeley and Zedler, 1998). There is no rigid demarcation between phases; rather, each phase transitions gradually to the next. Nonetheless, these phases provide a useful framework for studying temporal variation in plant and animal communities of vernal pools. In CVPs, the aquatic phase usually occurs between November and April, during which time the pools hold rainwater. Most plants in pool basins germinate during this phase but grow slowly as the rainy season progresses. The terrestrial phase begins when the rains cease in the spring and pools start drying. This phase usually occurs from late-April through May. A vascular-plant community consisting of annual native forbs and grasses dominates the terrestrial phase (Holland and Jain, 1981; Stone, 1990). These species vary in their germination and growth phenologies (Bliss and Zedler, 1998), but in general most species grow rapidly and flower during the terrestrial phase (Bliss and Zedler, 1998; Bauder, 2000). Once the soil is fully desiccated, pools enter the drought phase of summer and fall. Little biological activity is evident in pool basins during this time, but most organisms of the aquatic and terrestrial phases lie dormant as cysts and seeds in the soil awaiting the next rainy season (Holland and Jain, 1981).

Using mesocosms lined with vernal pool soil, we investigated the effects of cattle dung and urine on the water quality and vascular plant communities of California vernal pools. We focused on measuring variables in the terrestrial phase. Since most vascular plants grow rapidly and flower during this phase, any effects of cattle waste on vernal pool plants should be most evident during this phase. We predicted that the excess nutrients brought into the pools by dung and urine during the aquatic phase would result in eutrophication and greater biomass of filamentous and charophyte algae. We expected that these algae would aggregate into mats as the pools dried, and that these mats would negatively affect the percent-cover and species richness of terrestrial-phase vascular plants. Support for these predictions could place a contingency on the notion that properly managed grazing promotes plant diversity on grasslands, as this notion may not apply to vascular plants living in pool basins.

#### 2. Methods

#### 2.1. Experimental design

We arranged mesocosms in a blocked  $3 \times 2$  factorial design in a temperaturecontrolled greenhouse on the campus of California State University, Sacra-

#### Table 1

Approximate N and P loading rates (in g m<sup>-2</sup> d<sup>-1</sup>) into mesocosms for each treatment. Rates were calculated on the basis of waste-output characteristics published in ASAE Standards D384.1 (February 2003) and D384.2 (March 2005), and in Kolay (2007).

Treatment	Total N	Total P
Control (no urine or dung)	-	-
No urine, low dung	0.02	0.02
No urine, high dung	0.12	0.09
Low urine, no dung	0.06	0 <sup>a</sup>
Low urine, low dung	0.09	0.02
Low urine, high dung	0.18	0.09

<sup>a</sup> Urine contributes a negligible amount of P (Kolay, 2007). Therefore, all P input into our mesocosms is assumed to come from dung.

mento (mean ± SD temperature during the experiment =  $21.3 \pm 2.4 \,^{\circ}$ C, range = 15.6–25.2 °C). We used three levels of dung input (none, low, high) and two levels of urine input (none, low). Each of the six treatments had four replicates, for a total of 24 mesocosms. The mesocosm containers were white, 13.25L food-grade plastic buckets, 30 cm diameter × 28 cm tall. Dry soil was collected from a natural vernal pool complex in Sacramento County (Kneitel and Lessin, 2010), crushed to a fine consistency and homogenized. Each mesocosm containers were then filled to a depth of 22 cm with well water, for a total "pool" volume of 0.016 m<sup>3</sup>. This volume was maintained with weekly water additions. While our mesocosms differed markedly from natural pools in both total volume and surface area:volume ratio, recent evidence indicates that these factors have little effect on the response of aquatic communities to eutrophication (Spivak et al., 2010). Nonetheless, the size of our mesocosms was small compared to natural vernal pools.

We allowed the mesocosms to equilibrate for 4 weeks. Thereafter, we added treatments to the mesocosms every 2 weeks for 8 weeks. After 10 weeks, we took water quality measurements, then allowed the mesocosms to begin drying naturally. After they partially dried, we quantified filamentous algal biomass by scraping exposed periphyton from mesocosm sidewalls. In the late-terrestrial phase, when all standing water was gone but the soil still moist, we measured percent-cover of algae (filamentous and charophyte algae), percent-cover of vascular plants, and species richness of vascular plants.

#### 2.2. Treatment levels

For each treatment addition, we collected fresh dung from range-fed beef cattle and added it to the mesocosms within 2 h of collection. We obtained urine by draining the bladders of two slaughtered beef cattle. Aliquots of 30 mL were stored frozen at 0°C and thawed in hot water immediately prior to use. We added dung and urine to the mesocosms concurrently. A control treatment received no inputs.

The low-dung treatment used 8 g dung, and the high-dung treatment used 40 g dung. The low-urine treatment used 5 mL urine. Relative to the volume of our mesocosms (0.016 m<sup>3</sup>), these amounts represented 10 defecations, 50 defecations and 11 urinations, respectively, as determined on the basis of waste output quantities ascertained from literature reports (White et al., 2001; Aland et al., 2002) and Standards D384.1 (February 2003) and D384.2 (March 2005) of the American Society of Agricultural Engineers (ASAE); and a "typical" pool volume of 36 m<sup>3</sup>, which we calculated using surface area and depth measurements from King et al. (1996; median volume of 47 m<sup>3</sup>) and Carl and Blumenshine (2005; mean volume of 25 m<sup>3</sup>). Approximate loading rates of N and P into each treatment are summarized in Table 1. Our treatment-level calculations used data for beef cattle wherever possible, as beef cattle production often involves grazing on large expanses of pasture, whereas dairy cows are typically kept close to milking facilities. On the basis of field observations, our treatment levels were realistic amounts for natural vernal pools when considered in the context of our input timing, which was once every 14 days.

#### 2.3. Water quality

We used an Oakton pH/CON 300 device to measure temperature, pH and conductivity, and an Oakton pH/DO 300 device to measure dissolved oxygen. These measurements were taken *in situ* in the early afternoon. In the laboratory, we used a Hach DR2800 spectrophotometer and LaMotte 2020i turbidity meter to quantify phosphate (as orthophosphate) and turbidity, respectively. We also quantified nitrate levels, but toward the end of the experiment we discovered that our water samples contained compounds, presumably iron native to the soil, that interfered with the nitrate protocol we employed. Our nitrate dataset was thus rendered unreliable.

#### 2.4. Algae and plant variables

After the mesocosms began drying and water levels declined by roughly 6 cm, we used a 3.8 cm razor blade to scrape the exposed periphyton from the inner sidewall.



**Fig. 1.** Effect of dung on (a) dissolved oxygen, (b) phosphate, (c) turbidity, and (d) conductivity in vernal pool mesocosms (mean ± SE) after 10 weeks of treatment. Different letters above bars indicate a significant difference between treatments; same letters indicate no difference. Turbidity in this figure uses untransformed data. See Table 2 for the method of transformation and for ANOVA results.

We scraped one circumference of the sidewall just above the water surface. We airdried the collected periphyton in the greenhouse for three days before weighing. The periphyton undoubtedly contained bacteria and planktonic algae, but filamentous algae comprised the bulk of it. We thus reasoned that the biomass of this periphyton could serve as a proxy for the biomass of filamentous algae in the mesocosms (see Pettigrew et al., 1998). Collecting algae this way allowed us to sample algal biomass destructively but without influencing the submerged mesocosm community. Algal biomass (dry weight) is expressed in g m<sup>-2</sup> to facilitate comparison with the literature.

When all standing water was gone but the soil still moist, we estimated the percent-cover of filamentous and charophyte algae, which were by far the dominant algal groups in our mesocosms. We summed the percent-covers of these two groups into a single measure of algal percent-cover. We also identified each vascular plant species present and estimated its percent-cover. Total plant percent-cover in each mesocosm was calculated as the sum of the percent-covers of all vascular plant species present. The percent-cover of both algae and plants could exceed 100% due to intertwined mats and overlapping canopies, respectively. Plant species richness was measured as the number of vascular plant species present.

#### 2.5. Data analysis

All dependent variables were analyzed using two-way analysis of variance (ANOVA) with Bonferroni post hoc tests, with dung and urine as the fixed effects. When necessary, data were transformed to meet assumptions of normality and equal variance. We also conducted Pearson's correlations among water quality variables. We conducted these analyses in SPSS 16.0 for Mac.

To test whether vascular plant composition differed among treatments, we conducted one-way analysis of similarity (ANOSIM) with all six dung and urine treatments. The data matrix was based on species cover in each replicate of each treatment. We ran 5000 permutations and used Bray–Curtis distances. This analysis was conducted in the software package PAST 1.94b (Hammer et al., 2001).

## 3. Results

We found no effect of urine on any variables, whereas dung had a strong effect on most variables. In general, water quality was affected only by high-dung input, whereas algae and plant variables were affected by both low- and high-dung input. With one exception, we found no interaction between urine and dung.

### 3.1. Water quality

The high-dung treatment had lower dissolved oxygen (Fig. 1a), greater phosphate (Fig. 1b), higher turbidity (Fig. 1c), and higher conductivity (Fig. 1d) compared to the no-dung treatment. These differences were significant (Table 2) and confirmed our expectation that dung input would shift water quality toward a eutrophic state.

In both dung treatments, pH declined. This decline was statistically significant (Table 2) but very small, and values remained within the range found in natural vernal pools (King et al., 1996). In the high-dung treatment, pH was  $7.9 \pm 0.1$  (mean  $\pm$  SE), compared

#### Table 2

ANOVA summary for the effects of dung and urine on water physicochemistry, algae, and vascular plant variables of vernal pool mesocosms. For all analyses, numerator degrees of freedom (DF) were 2, 1, and 2 for dung, urine, and the interaction term, respectively. Denominator (error) DF were 18.

Variable	Dung		Urine		Dung × Urine	
	F-value	<i>P</i> -value	F-value	P-value	F-value	<i>P</i> -value
Dissolved oxygen (mg/L)	68.1	<0.001	3.83	0.07	0.71	0.50
Phosphate (mg/L) <sup>a</sup>	655.8	< 0.001	0.00	1.00	0.57	0.58
Turbidity (NTU) <sup>b</sup>	12.7	< 0.001	0.06	0.81	0.57	0.58
Conductivity (µS)	142.4	< 0.001	1.42	0.25	0.17	0.85
pH <sup>b</sup>	25.9	< 0.001	0.31	0.58	0.45	0.65
Algal biomass (dry wt, g m <sup>-2</sup> )	3.52	0.05	0.33	0.57	0.84	0.45
Algae cover (%)	5.70	0.01	0.67	0.42	1.05	0.37
Plant cover (%) <sup>a</sup>	19.9	< 0.001	0.08	0.78	2.29	0.13
Plant species richness	13.7	< 0.001	0.97	0.34	2.84	0.08
Eleocharis macrostachya cover (%)	10.9	0.001	2.58	0.13	1.81	0.19
Marsilea vestita cover (%)	4.16	0.03	0.02	0.89	4.05	0.04
Ranunculus bonariensis cover (%)	17.2	<0.001	0.10	0.76	0.30	0.74

<sup>a</sup> Square-root transformed.

<sup>b</sup> Rank transformed.



**Fig. 2.** Effect of dung on (a) algal biomass, (b) algae percent-cover, (c) vascular plant percent-cover, and (d) vascular plant species richness in vernal pool mesocosms (mean  $\pm$  SE) in the late-terrestrial phase. Different letters above bars indicate a significant difference between treatments; same letters indicate no difference. Plant percent-cover in this figure uses untransformed data to more clearly show differences between treatment groups. See Table 2 for the method of transformation and for ANOVA results.

with  $8.4 \pm 0.1$  in the low-dung treatment and  $8.7 \pm 0.1$  in the no-dung treatment.

Pearson's correlations revealed several notable relationships among water quality variables. Phosphate was positively correlated with conductivity (r=0.97, P<0.001) and negatively correlated with pH (r=-0.76, P<0.001) and dissolved oxygen (r=-0.91, P<0.001). Dissolved oxygen was negatively correlated with conductivity (r=-0.89, P<0.001) and positively correlated with pH (r=0.84, P<0.001). Turbidity was negatively correlated with pH (r=-0.45, P=0.03).

## 3.2. Algae and plant variables

As a result of nutrient enrichment, algal biomass in both dung treatments increased greatly compared to the control (Fig. 2a), and this difference was significant (Table 2). Algal cover was significantly higher in the high-dung treatment than in the no-dung treatment (Table 2). Compared to the no-dung treatment, this cover increased by 53% in the high-dung treatment (Fig. 2b).

We observed a total of 8 vascular plant species in our mesocosms (Table 3). The species observed are typical of vernal pools in northern California (Barbour et al., 2007). The number of vascular plant species in each mesocosm ranged from 1 to 7. Plant cover and species richness were significantly lower in the dung treatments than in the no-dung treatment (Table 2). Compared to the no-dung treatment, plant percent-cover decreased by 87% in the high-dung treatment and by 69% in the low-dung treatment (Fig. 2c). Plant species richness in the high-dung treatment decreased by 54% compared to the no-dung treatment (Fig. 2d). Vascular plant composition was significantly different among dung and urine treatments, but these differences were comparatively small (Global ANOSIM: R=0.28; P=0.005). In general, low-nutrient treatments were significantly different from highnutrient treatments. The control treatment (no dung/no urine) was significantly different from both high-dung treatments (i.e., dung added with and without urine) and the low-dung/low-urine treatment. Further, the no-dung/low-urine treatment was significantly different from the low-dung/low-urine and high-dung/low-urine treatments. These compositional differences were reflected in the species' percent-covers. The percent-covers of three vascular plant species (Eleocharis macrostachva Britton, Ranunculus bonariensis Poir., and Marsilea vestita Hook. & Grev.) significantly decreased with dung addition (Table 2). A dung  $\times$  urine interaction was found with M. vestita, whereby urine increased this species' percent-cover in the absence of dung.

## 4. Discussion

Adding high but realistic amounts of cattle waste to vernal pool mesocosms during their aquatic phase caused an 87% decrease in plant percent-cover and a 54% decrease in plant species richness in the subsequent terrestrial phase. Also, the composition of the terrestrial-phase plant community shifted with the dung treatments. We attribute these results to the proliferation of filamentous and charophyte algae during aquatic-phase nutrient enrichment. These algae formed dense mats in the high-dung mesocosms, which

Table 3

Vascular plant taxa observed in mesocosms. Except for the unidentified grass, these taxa are typical of those found in vernal pools in northern California (Barbour et al., 2007). Percent-occurrence by treatment pertains to dung levels only (urine had no effect on any variables) and is based on 8 replicates per treatment.

Taxon	Description	% Occurrence by dung treatment		
		None	Low	High
Eleocharis macrostachya Britton	Native monocot	100	75	87.5
Ranunculus bonariensis Poir.	Native, endemic dicot	87.5	62.5	75
Plagiobothrys stipitatus Greene I.M. Johnst.	Native, endemic dicot	100	50	37.5
Marsilea vestita Hook. & Grev.	Native fern	62.5	50	12.5
Gratiola ebracteata Benth. ex A. DC.	Native dicot	12.5	12.5	0
Lythrum hyssopifolia L.	Introduced dicot	50	37.5	0
Unidentified grass	_	37.5	12.5	0
Ranunculus aquatilis L.	Native dicot	37.5	0	12.5

likely prevented light from reaching the submerged plants during a critical time in their life cycle. Our results suggest that regardless of the effects of grazing on plant diversity at the regional scale, grazing may be detrimental to plant diversity within pool basins. These results stand in contrast to those of recent studies examining the effects of grazing on plant diversity in grasslands (Towne et al., 2005; Brudvig et al., 2007; Johnson and Cushman, 2007), including those that contain vernal pools (Marty, 2005).

The attenuation of light by algae has been documented in other studies. Ozimek et al. (1991), for example, found that the filamentous alga Cladophora glomerata reduced light in experimental chambers by 30-80% and negatively affected the growth of two freshwater macrophyte species. Moreover, in estuaries the lightattenuating effect of epiphytic algae on seagrass is well established (Sand-Jensen, 1977; Brush and Nixon, 2002). In California vernal pools, Zedler (1987) suggested that filamentous algal mats might increase plant mortality via light attenuation. It is not uncommon to observe such mats in vernal pools, and on grazed grasslands they can be extensive (R. Croel and J. Kneitel, personal observations). These mats probably function similarly to thatch (i.e., litter biomass) in terrestrial systems. Thatch also increases in response to nutrient enrichment (Foster and Gross, 1998) and at high levels can inhibit plant germination, survival, and species richness on grasslands through light attenuation (Hautier et al., 2009). We cannot definitively attribute the observed effects on the plant community to light attenuation by algal mats due to our study design. Nevertheless, we suspect it was the main cause given the known effects of algae-driven light attenuation on aquatic plants as well as the extensive cover of algal mats in the dung-treated mesocosms. Planktonic algae probably contributed little to light attenuation, as our turbidity results suggest that they did not reach high population densities. This was likely due to herbivory by suspension-feeding invertebrates. Indeed, the population densities of these taxa, especially cladocerans and ostracods, increased rapidly in the dung-treated mesocosms (R. Croel and J. Kneitel, unpublished data), and this probably moderated the phytoplankton response.

Besides light attenuation by algal mats, several alternative explanations could account for the change in vascular plant composition, cover, and species richness. First, nutrients or other water quality parameters that were not measured, especially nitrate and ammonium, could have influenced species composition through resource competition between algae and plants (e.g., Van Donk and Van de Bund, 2002). This could explain why vascular plant variables were affected by both the low- and high-dung treatments, but water quality variables (except turbidity) were affected only by the high-dung treatment. Evidence regarding the effects of added nitrogen on macrophytes is mixed, however, and ultimately such effects may be a function of the N:P ratio or total phosphorus (e.g., Smith, 1982; Elser et al., 2007; Li et al., 2008; Özkan et al., 2010). Second, changes in water quality, either directly or in combination with increased algae, may have mediated competitive interactions between plant species (Dunson and Travis, 1991), resulting in compositional shifts. Third, the stress of desiccation may have interacted with treatment effects to differentially affect species. For example, wetland plant species can vary in their response to combinations of nutrients and hydroperiod (e.g., Newman et al., 1996; Miao et al., 2009). While variation in hydroperiod can affect vernal pool species composition (Bliss and Zedler, 1998; Bauder, 2000), this explanation is unlikely here since our mesocosms experienced the same hydroperiod. Moreover, vascular plant species associated with vernal pools are morphologically and physiologically adapted to the annual inundation-desiccation cycle (Keeley, 1990; Stone, 1990)

Because they are filled primarily by rainwater, vernal pools are generally oligotrophic systems (Keeley and Zedler, 1998). Even small amounts of nutrient input may therefore have considerable consequences to community structure. Our results support this assertion. The high-dung treatment had a clear impact on plants, algae, and water quality. The low-dung treatment had little impact on water quality but its effects on plants and algae were comparable to the high-dung treatment, suggesting that plants and algae in vernal pools may be extremely sensitive to nutrient enrichment. Ultimately, however, whether cattle waste poses a threat to plants in natural pools depends on how other aspects of grazing, namely phytomass removal and trampling, interact with waste deposition to produce a net effect. Focusing on just one aspect of grazing, as we did in this study, is unrealistic for natural vernal pools; cattle cannot excrete into pools unless they are standing in them, in which case trampling will also occur, and possibly phytomass removal as well. Nonetheless, understanding how the different components of grazing separately impact vernal pools can augment our understanding of how grazing as a whole impacts these pools.

Vernal pool habitat is declining worldwide (Ruiz, 2008; Serrano and Zunzunegui, 2008; Pinto-Cruz et al., 2009), and much of what remains is shared with grazing cattle. Clearly, the growing body of research (e.g., Cabin et al., 2000; Kimball and Schiffman, 2003; Marty, 2005; Rhazi et al., 2006; Bouahim et al., 2010), including the present study, illustrates the complex effects of cattle grazing on community- and ecosystem-level properties. Additional research on the longer-term effects of cattle grazing on vernal pools will prove crucial to understanding fully the effects of agricultural operations on these unique and increasingly threatened ecosystems.

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