AN INVESTIGATION OF POLLEN LIMITATION AND SEED VIABILITY IN
LASTHENIA FREMONTII IN CONSTRUCTED AND NATURAL VERNAL POOLS

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Jessica Alexander

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Jahna Kneitel, Ph.D. 30 OCT 15

Department of Biological Sciences
Abstract of

AN INVESTIGATION OF POLLEN LIMITATION AND SEED VIABILITY IN LASTHENIA FREMONTII IN CONSTRUCTED AND NATURAL VERNAL POOLS

by

Jessica Alexander

Recent evidence of widespread declines in insect pollinator populations in the U.S. has raised extraordinary concern and has ushered the immediate need for more research on plant-pollinator interactions to better assess the magnitude of potential ecological and societal impacts. In California, vernal pools are seasonal wetlands host to several endemic annual plant species, many of which depend on pollination by native specialist bees for reproduction. Pollen limitation, or inadequate pollen receipt in plants, reduces viable seed production and consequently has the potential to impair the long-term persistence of annual plant populations in vernal pools. Across California, the construction of vernal pools is a common habitat mitigation strategy to offset impacts from urban and agricultural developments. Yet, few studies have examined pollen limitation and pollinator foraging frequency in plant populations of constructed vernal pools.

Based on previous studies, I hypothesized that there would be greater pollen limitation in Fremont’s goldfields (Lasthenia fremontii), a common endemic annual, in
constructed versus natural vernal pools in Placer County, California. I tested this hypothesis by 1) measuring pollen limitation and seed viability in *L. fremontii* in constructed and natural vernal pools; 2) for individuals in which pollen limitation was measured, I recorded plant height and the number of inflorescences as well as local site characteristics including population abundance of *L. fremontii*, the timing of flowering, and elevation within the pool; and 3) collected observations of pollinator visits to *L. fremontii* in constructed and natural vernal pools. Pollen limitation indices were calculated for plant pairs from both pool types by comparing two treatments: open-pollinated (control) *L. fremontii* plants with those that received pollen supplementation via hand pollination.

I found no support for my hypothesis. Mean pollen limitation per pool was low in both constructed and natural vernal pools and no statistically significant difference was found between groups. This finding suggests that pollen delivery to *L. fremontii* by pollinators was similarly effective in both the constructed and natural vernal pools during the study period. Furthermore, observations of pollinator foraging revealed that generalist, opportunistic insects comprised the majority of visitors to *L. fremontii*; no native specialist bees were observed visiting *L. fremontii*.

Plant species richness in vernal pools was positively associated with the percent viable *L. fremontii* seeds in the constructed and natural pools; while, plot elevation and maximum percent cover of *L. fremontii* had negative effects on the percent of viable seeds. The relationship between species diversity and increased biomass production, as shown for *L. fremontii*, and previously demonstrated by others (Cardinale et al. 2007,
Hector et al. 1999), is valuable to the field of vernal pool restoration ecology, especially considering the loss of vernal pool habitat seen in recent decades throughout California.

Thirty-nine percent of the *L. fremontii* plants monitored for this study were wholly or partially damaged by cocooning and/or herbivory caused by the sunflower moth caterpillar (*Homoeosoma* sp.). This invasive moth has the propensity to cause ecological damage to fragile vernal pool ecosystems in California. Further research is needed to understand and attempt to quantify the impacts of *Homoeosoma* sp. on non-cultivated Asteraceae populations where found in vernal pools, open grasslands, and roadside areas in the Central Valley.

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Jaime Kneitel, Ph.D.

30 Oct 15

Date
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A special thanks goes to Dr. Shannon Datwyler for assisting early on in the development of this study and for sharing her enthusiasm for botany, which led me to discover my own passion for plants. Thank you to Dr. Ronald Coleman, Dr. Patrick Foley, and Dr. Nancy Emery for providing guidance and also thanks to my field assistants Merrill Roseberry and Lindsay Peterson. I am grateful to Nell Conti who helped with the GIS mapping for this study.

I dedicate this thesis to my mother, Susan Griggs, who inspired me to pursue a Master’s degree at a young age. Finally, and most importantly, I could not have completed this project without the limitless source of strength, balance, and support from my husband Charlie Alexander.
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INTRODUCTION

Considerable concern has arisen over the past decade that pollinator communities are in jeopardy on account of rapid declines in pollinator populations (Lebuhn et al. 2012, Biesmeijer et al. 2006, Potts et al. 2010). Habitat loss and fragmentation, the widespread use of pesticides, and the replacement of natural plant communities with agricultural monocultures represent only a partial list of stressors that render significant alterations to the environment that in turn threaten native pollinator communities (Cane and Tepedino 2001). Determining the severity and extent of impacts caused by these and other human-induced changes to the environment and whether they will result in interactive, cumulative, or irreversible effects to native pollinators have become pressing questions. Moreover, researchers face many challenges in studying plant-pollinator interactions due to the inherent variation in pollinator abundance and detection (Lebuhn et al. 2012). Therefore, there is a pressing need to investigate the magnitude of declines by assessing plant-pollinator interactions. For example, studies on pollinator foraging and pollination deficits in plants are two approaches for examining evidence of pollinator declines (Cane and Tepedino 2001).

One approach to assess pollinator availability, frequency of visitation, and effectiveness of pollen transfer is to study pollen limitation in plants. Pollen limitation occurs when plants produce fewer fruits and/or seeds than they would with adequate pollen receipt (Knight et al. 2005). Inadequate pollen receipt, due to a deficiency in the quantity of pollinator visits or the quality of compatible pollen transfer during visitation, has both ecological and evolutionary ramifications (Ashman et al. 2004).
Ecological effects of pollen limitation can shape species coexistence (Ishii and Higashi 2001), community structure, and ecosystem functioning (Bond 1994, Amarasekare 2004). Pollen limitation in plants may decrease population abundance, cause shifts in population demography and structure, or ultimately result in population declines leading to species extinction (Ashman et al. 2004). Pollen limitation may decrease the absolute or relative abundance of a species, which could shift the community to one dominated by species that are less prone to pollen limitation such as self-pollinating species (Ashman et al. 2004, Moeller and Geber 2005, Aizen and Harder 2007). Self-pollination adaptations decrease pollen limitation and promote future reproductive assurance (Ashman et al. 2004).

In contrast, for exogamous (non-self pollinating or obligate out-crossing) species, pollen limitation on seed production has the propensity to negatively impact entire populations, the effects of which may be realized across many flowering seasons. For annual plant species in particular, viable seed production and deposition in the seed bank are necessary to ensure long-term population survival (Sloop et al. 2012). Therefore, the effects of pollen limitation on seed production in annual plant species could consequently impair long-term species persistence.

In California, vernal pools are seasonal wetlands formed by shallow depressions in the landscape, which sit atop an impervious hardpan soil layer that causes temporary ponding of rainwater (Holland and Jain 1981). In a given year, vernal pools typically experience a wet phase, a flowering phase, and a dry phase. Many annual plant species of the genera *Blemnosperma*, *Downingia*, *Lasthenia*, and *Limnanthes*, whose showy
floral displays are characteristic of California’s vernal pools, depend on adequate pollination wholly or in part by oligolectic or specialist bees of the family Andrenidae for successful reproduction (Thorp and Leong 1998). These specialist bees forage in the flora-rich vernal pool basins and nest in the terrestrial upland matrix, therein providing an ecological link between the terrestrial uplands and low lying aquatic vernal pools (Thorp and Leong 1998).

The ephemeral nature of vernal pools allows these environments to support unique flora and fauna, the loss of which has become a topic of conservation concern across the state in recent decades as increases in urban development and agricultural land conversions threaten vernal pool habitat. Historically thought to be widespread throughout the Pacific Coast and California’s Central Valley, it is estimated that only three to ten percent of historic vernal pools remain due to habitat loss (Holland and Jain 1988, Holland 1998). Restoration projects that enhance vernal pool plant communities by reintroducing native annuals and creating vernal pool habitat are key to promoting vernal pool recovery (Collinge and Ray 2009).

While beneficial, constructed vernal pools constitute recently colonized communities that lack an established seed bank and often the health and makeup of the local pollinator community is unknown. For these reasons, the creation of vernal pools in an environment where none had been previously has the potential to result in fewer or less effective pollinator visits (Schiller et al. 2000). For example, specialist solitary bee pollinators may not be as abundant near constructed pools as they are at less disturbed, natural vernal pools (Sloop et al. 2012). Constructed vernal pools have become common
vehicles for wetland mitigation in California; however, presently there is little research on pollen limitation and pollinator foraging frequency on annual plants of constructed vernal pools.

In response to conservation concerns, several field studies have been undertaken to estimate occurrences of pollen limitation in vernal pool systems; yet, the breadth of the existing research is limited. For example, in *Lasthenia fremontii* (Fremont's goldfields) Emery (2009) observed increased seed set in early flowering plants as compared to later flowering plants in natural vernal pools located in Sacramento County, California. Early flowering individuals were at an advantage for pollinator services as evidenced in observations of the flight paths of foraging pollinators, which were restricted within narrow microelevational limits among the flowering population at the pool level (Emery 2009). In an earlier study Emery (2006) reported that changes in pollinator flight paths likely followed the transitioning stages of flowering as water level recedes down the elevation gradient in a vernal pool. This could be explained by the fact that the plants beginning to flower are likely to have higher nectar and pollen loads than those plants at higher, drier microelevations and are therefore highly attractive to pollinators.

For the medium-sized natural pools that were studied by Emery (2009), the deepest centers of the pools contained the highest density of *L. fremontii* individuals, which had higher seed set and reduced pollen limitation; in contrast, edge individuals had lower seed set and increased pollen limitation. The observed *L. fremontii* densities were partially attributed to moisture levels and the shifting hydrological regime of retreating water levels during the onset of the drying phase experienced in vernal pools (Emery 2009).
However, these findings demonstrated that conspecific population density and microelevation are factors that influence the frequency of pollinator visitation in systems where pollinator availability is sufficient.

Sloop et al. (2012) conducted a field study to examine plant-pollinator ecology in three state and federal listed endangered plant species: *Lasthenia burkei* (Burke's goldfields), *Blennosperma bakeri* (Sonoma sunshine), and *Limnanthes vicularis* (Sebastopol Meadowfoam) in natural and constructed vernal pools located in Sonoma County, California. For *L. burkei*, *B. bakeri*, and *L. vicularis* populations exceeding 35 percent cover, increased seed set was observed in all three species. While the authors found evidence of decreased seed set at the study sites between years and among constructed and natural pools, there was no statistically significant difference in seed set in *L. burkei* in constructed versus natural vernal pool types but there were differences in seed set among pools. A pertinent finding of this study was that observations of the number of pollinator visits were lower in created vernal pools than natural pools for all three target plant species, which is likely indicative of lower abundance and accessibility of the local pollinator community to each of the created pool sites.

The ecological context in which plants experience pollen limitation is an area ripe for study in which much is still unknown (Moeller and Geber 2005). For this study I examined the degree to which pollen limitation can be attributed to pollinator visitation and environmental conditions in constructed and natural vernal pools. My primary goal was to improve scientific understanding of plant-pollinator interactions under different environmental conditions (constructed and natural vernal pools), using *L. fremontii* as a
focal species. Knowledge gained from this study may be used to inform natural resource management decisions regarding vernal pool conservation and the creation of vernal pool habitat.
METHODS

Study Site

The field portion of this study was conducted at the Teichert Lincoln Property in Placer County, California (38°58'44.0"N, 121°18'37.2"W), which is owned and managed by Teichert Aggregates. The Teichert Lincoln Property contains a contiguous wetland complex of constructed and natural vernal pools encompassing approximately 143 acres (57.9 hectares) (Teichert Aggregates 2009). Sixty-one vernal pools totaling 8.05 acres (3.3 hectares) were constructed in September of 1997 in anticipation of future mitigation for wetlands that would be impacted by Teichert’s proposed aggregate facility. Constructed pools were built on natural claypan and monitored for a total of six years during an 11-year period following construction. A monitoring program and success criteria were established, and the final year monitoring report concluded that 58 of the 61 vernal pools met all vegetation success criteria. By the final monitoring year in 2008, the constructed vernal pools were observed to support typical Sacramento Valley vernal pool species and showed similar vegetation characteristics in terms of species richness and composition to the natural reference vernal pools on the property (Teichert Aggregates 2009).

Focal Species

*Lasthenia fremontii* was chosen for this study due to the breath of existing research available on this species, including successful pollen supplementation experiments performed by Sargent et al. (2011) and Emery (2006, 2009). Commonly known as
Fremont's goldfields, *L. fremontii* is a self-incompatible, annual plant endemic to vernal pools of California's Central Valley (Sargent et al. 2011). Plants typically produce a single terminal inflorescence but may produce additional inflorescences (Sargent et al. 2011). Each inflorescence has a yellow corolla made up of 6 to 13 ray flowers and many individual disk flowers (Baldwin et al. 2012). Flowering typically occurs for approximately six to eight weeks (Sargent et al. 2011) between March and May (Baldwin et al. 2012). In this study, *L. fremontii* plants were identified using the Jepson Manual: Vascular Plants of California, Second Edition (Baldwin et al. 2012).

Pool Selection

As similar to past years, cattle grazing pastures were rotated throughout the Teichert Lincoln Property during the winter months. All cattle were removed from the site in early March 2014. At this time, prior to the start of *L. fremontii*’s flowering period, I identified suitable vernal pools for this study using the following resources: ArcGIS shapefiles of onsite vernal pools, historic satellite aerial photographs, Teichert Aggregates aerial maps, and plant species data collected by Teichert Aggregates for the years 1997 to 2008, which revealed pools with recorded occurrences of *L. fremontii*.

An initial goal in selecting natural and constructed vernal pools for this study was to standardize for size. In ArcGIS, I used shapefile data of all the vernal pools onsite (natural and constructed) to examine their respective acreages. Over the winter months and continuing through March 2014, the Sacramento region had experienced very little rainfall and onsite vegetative conditions at the Teichert Lincoln Property were atypically
dry for the time of year. I visited the study site approximately every three days from March through early April to monitor occurrences of *L. fremontii* in bloom. The first *L. fremontii* open blooms I observed onsite occurred in a natural pool located near the point of highest elevation on the property on April 15, 2014. During the final days of April, the study site experienced temperatures reaching 32 degrees Celsius (90 degrees Fahrenheit).

Ten natural and 10 constructed vernal pools were selected for the study. An aerial map of the 20 vernal pools is shown in Figure 1.

The study site occurs within a larger watershed wherein the landscape gradually decreases in elevation from north to south, conveying surface water flows towards the south of the site. The timing of the first blooming *L. fremontii* generally coincided with the timing of water levels receding and the margins of the vernal pools drying out, which first occurred in the natural pools located in the upper portion of the watershed. The constructed pools occur in the southern end of the site, which is generally located at a lower point of elevation in the watershed. For all 20 pools, the timing of first flowering in *L. fremontii* typically occurred later in constructed pools than in the natural pools (Figure 2).
Figure 1. Aerial map of the study site with natural and constructed vernal pools shown. Teichert Aggregates Lincoln Property (38°58'44.0''N, 121°18'37.2''W), located eight miles north of the city of Lincoln in Placer County, California.
Figure 2. A comparison of the mean date of first flowering of *L. fremontii* in plots shown by pool type. Generally, *L. fremontii* plants in the natural pools were observed to bloom earlier than those plants in the constructed pools.
Plots

For each of the vernal pools, a transect was placed along the greatest length of the pool and a random point was selected on the transect. From this randomly selected point, a second transect was placed perpendicular to it and from which a second random point was selected along the second transect. This second point became the final location where the plot (quadrat) was placed inside the pool if the location contained *L. fremontii* plants. This process was repeated for a total of eight randomly selected plots in each pool.

To achieve a greater representation of *L. fremontii* plants at varying percent cover densities, plot locations were initially established such that two plots per pool were representative of the following *L. fremontii* cover categories: 20-40%, 40-60%, 60-80%, and 80-100%. Due to the rapid desiccation of vegetation that occurred across all of the pools during the study period, some plots had to be moved within the pool to where fresh *L. fremontii* were remaining. Plot selection began on April 22, 2014 and percent cover estimates of *L. fremontii* were performed for each plot and repeated every two to four days per Emery (2006), for the duration of the flowering period for all 20 vernal pools.

Percent cover of *L. fremontii* was calculated using a 0.25 m² quadrat divided into a grid with 5 cm spacing between grid points using string. The quadrat was placed over the vegetation and percent cover of flowering *L. fremontii* was visually estimated for the plot. Species richness was also measured for each plot. Photographs of plots were taken each day the percent cover and species richness estimates were conducted. The photographs were reviewed following the completion of the field study to verify species richness.
estimates. Once flowering subsided in all eight plots in each pool, the elevation of each plot relative to the bottom of its respective pool was measured to the nearest centimeter using an auto level (Emery 2006).

Pollen Supplementation

Once flowering began, for each plot, one *L. fremontii* plant was selected using random coordinates on the quadrat. The selected plant was assigned to receive pollen supplementation treatments every two to three days for the duration of the flowering period (Emery 2009) with the intent to supersaturate the flower head with donor pollen. Per Sargent et al. (2011), *L. fremontii* inflorescences within 10 meters outside the experimental plots were used as pollen donors to the extent that they were readily available and time permissible. All pollen donor *L. fremontii* plants were selected from outside of the plots. Hand pollination supplementations were conducted by gently brushing the donor inflorescence over the recipient inflorescence in the experimental plot (Sargent et al. 2011, Emery 2006 and 2009). If a recipient plant had more than one inflorescence, then the pollen supplementation was repeated for the additional inflorescences (Sargent et al. 2011, Emery 2006 and 2009). The pollen-supplemented plants were marked with a colored bird band, which wrapped around and rested at the base of the plant stem (Emery 2006).

For each hand-pollinated plant, a *L. fremontii* plant of similar size and in close proximity was also marked with a different colored bird band inside the respective plots to serve as a control. Plant “pairs” consisted of one hand-pollinated plant and one open-
pollinated (control) plant in each plot. In total, 16 plants (eight hand-pollinated and eight open-pollinated) were monitored in each of the 20 vernal pools.

In each plot, if the random coordinate selected on the quadrat produced a location without a L. fremontii plant, the next closest L. fremontii plant was selected. If the selected L. fremontii flower was already open in full bloom or if a second L. fremontii plant nearest in the plot of the same age and height to be used as a control could not be found, then the entire plot location was moved to the next nearest pair of L. fremontii that exhibited similar heights and similarly sized unopened buds. The L. fremontii pair in each plot was marked with bird bands before the focal inflorescence on each plant was open.

Due to the atypical dry conditions and warm temperatures, several of the plot locations had to be re-adjusted within the pools to avoid desiccated vegetation patches and to select an appropriate L. fremontii pair of the same age. Hand pollinations occurred for plots within each pool every two to three days; however, due to the rapid desiccation of vegetation in the pools some pools received more hand pollination treatments than others depending upon local site conditions and the rate of drying experienced in each pool.

Every two to three days the degree of maturation of the L. fremontii plants was assessed to ensure collection at the appropriate time as the plants begin drying up, which is evident when the sepals peel back, the ray flowers are clearly gone, and the disk flowers have begun to shrivel and no longer appear to function for the attraction of pollinators (Emery pers. comm. 2013). Once the fruits were visibly mature but before
dispersal, all of the banded hand-pollinated and open-pollinated plants in each of the 20 vernal pools were collected. Plants were collected by clipping them at the base of the stem at the soil surface. Each collected plant was placed in an envelope upon which its location information was inscribed.

The number of hand-pollinated and open-pollinated plants totaled 16 from each pool, for a grand total of 319 plants collected from all 20 pools. The inflorescence of one *L. fremontii* plant was missing and could not be found at the plot location.

After all the plants were collected and the field portion of the study was complete, plant height was measured and the number of inflorescences was recorded for all of the *L. fremontii* plants collected. Using a dissecting scope, the total number of ovules from the focal inflorescence of each plant was recorded as the sum of viable and inviable seeds (Emery 2006). The inviable seeds were distinguished by their pale, white, withered appearance, which is in contrast to the dark brown, full achenes of viable seeds (Emery 2009).

A pollen limitation index (PLI) was calculated for the plant pairs in each plot using the formula $\text{PLI} = 1 - \frac{P_o}{P_s}$, where $P_o$ is the percent fruit set of open pollinated controls and $P_s$ is the percent fruit set by plants that received supplemental pollen (Larson and Barrett 2000, Weston et al. 2012). A pollen limitation index of zero indicates no pollen limitation in the population under study, whereas a pollen limitation index of one indicates complete pollen limitation (Larson and Barrett 2000, Weston et al. 2012). For pollen limitation index values less than zero, a zero was substituted in the dataset.
Observations of Pollinator Visitation

Pollinator observations were conducted on May 3, 5, 6, and 7, 2014 to compare visual estimates of pollinator foraging activity on *L. fremontii* plants between constructed and natural vernal pool types. One to three volunteer assistants accompanied me in the field each observation day to observe pollinator activity over the course of ten-minute observation periods. All pollinator landings or “visits” on the inflorescences of *L. fremontii* plants within the pool were treated uniformly as potential pollen transfer events. Observations of pollinator activity were recorded by slowly walking the perimeter of the pools and by stationary positions inside the pools. Due to low winter rainfall and warm spring temperatures, many pools experienced rapid desiccation and therefore pools were selected for observation based on a relative abundance of open blooms accessible for pollinators.

Over the course of the four observation days, a total of 31 unique observation periods were conducted from a sampling of the 20 natural and constructed vernal pools. To control for the effects of inclement weather on pollinator activity, observations were conducted during temperatures of at least 17 degrees Celsius (63 degrees Fahrenheit); although, temperatures exceeding 18 degrees Celsius (65 degrees Fahrenheit) provide improved conditions for pollinator foraging (Sloop et al. 2012). Due to the fact that the study site’s open grassland landscape is unimpeded by trees or other wind barriers, the study site experienced relatively high winds ranging from 13 to 23 kph (8 to 14 mph) during the observation days. Consequently, this negatively affected pollinator activity so
few pollinators were observed foraging in the vernal pools and in the surrounding upland areas.

To the degree feasible, the types of pollinators were recorded in the field according to generalist or specialist pollinator categories. Specialist pollinators include native bees in the family Andrenidae, which are solitary, ground-nesting bees that forage in vernal pools and use the pollen of specific vernal pool flowers to feed their young. Generalist pollinators include non-native bees and other insects that also visit vernal pool flowers and have the potential to pollinate them (Witham 2006).

During the pollinator observation days, three days included net sweep sampling of pollinators visiting *L. fremontii* using mesh butterfly nets. All collected insects were killed using plastic vials containing a small sponge wetted with Dicholvos, then labeled with locality information (and sample plot number). Dr. Patrick Foley, California State University, Sacramento, generously provided his assistance with insect collection, field observations, and taxonomic identification for this study. Identification of difficult bees was performed with the help of the collection at the Bohart Museum, University of California, Davis.

Caterpillar Cocooning and Herbivory

Caterpillars of the sunflower moth (*Homoeosoma* sp., Pyralidae) were observed causing damage to *L. fremontii* in my study pools. Powell and Opler (2009) describe 12 species of *Homoeosoma* that occur in western North America, which primarily feed on the flower tissue of Asteraceae plants. The sunflower moth (*Homoeosoma ellectellum*)
occurs across the continent and is widely known as an agricultural pest that infests commercial sunflowers (*Helianthus annuus*) (Powell and Opler 2009). Powell and Opler (2009) also note that other recorded host plants include a wide variety of other indigenous and cultivated Asteraceae, including thistles (*Carduus* and *Cirsium*), groundsel (*Senecio*) and coneflower (*Rudbeckia*) to name a few. To the best of my knowledge, *L. fremontii* has yet to be described in the literature as a host of *Homoeosoma*.

The size and markings on the *Homoeosoma* caterpillars were variable, as shown in the photographs in Appendix A. Of the total 319 *L. fremontii* plants monitored and collected for this study, 123 plants (39 percent) were wholly or partially damaged by *Homoeosoma* sp. cocooning and/or herbivory. Unfortunately, as a result, these plants were removed from further statistical analysis. The statistical analysis for the pollen supplementation experiment contains a smaller dataset of the remaining 196 plants void of caterpillar damage.

Often, only one cocoon was present on each *L. fremontii* inflorescence; however, I also saw plants with two cocoons per inflorescence. The cocoons were only observed on the inflorescences of *L. fremontii* plants, and not on any other plant species in the vernal pools. Unfortunately, caterpillar damage to the inflorescences of *L. fremontii* plants was extensive and was documented in 19 of the 20 vernal pools. Constructed Pool 18 was the only pool where no caterpillar damage occurred to any of the 16 *L. fremontii* plants under study. Photographs of a healthy *L. fremontii* inflorescence and one damaged by caterpillar cocooning and herbivory are shown in Appendix B.
To visually quantify the extent of damage to *L. fremontii* plants caused by *Homoeosoma* sp. cocooning and herbivory, a comparison of the damaged and undamaged plants collected from each pool is shown in Figure 3.
Figure 3. A comparison of the 16 L. fremontii plants collected from each pool showing those damaged and undamaged by Homoeosoma sp. caterpillars. Pools 1 through 10 represent the natural pools; Pools 11 through 20 represent the constructed pools. The inflorescence from one L. fremontii plant in Pool 16 was observed to be missing from its stem and could not be found.
Data Analysis

To determine if pool type (natural or constructed) had a significant effect on the observed site characteristics measured in all plots, specifically: timing of the first blooming \textit{L. fremontii} in plot by pool, plot species richness, plot elevation, and \textit{L. fremontii} plant height and number of inflorescences, I conducted several independent samples \( t \)-tests. Pollen limitation indices were calculated for the plant pairs in each plot using the formula $\text{PLI} = 1 - \left( \frac{P_o}{P_s} \right)$.

Since the pollen limitation data did not satisfy parametric assumptions, I performed a non-parametric Mann Whitney \( U \)-test to determine if the pool type environment (natural or constructed) had a significant effect on pollen limitation. Subsequently, I conducted an independent samples \( t \)-test to determine if the pollen supplementation treatments affected the number of viable seeds produced.

To investigate other factors that may affect seed set success in \textit{L. fremontii}, I conducted a stepwise (backward) regression analysis for the dependent variable percent of viable seeds and inserted the following independent variables:

- plot elevation within pool,
- \textit{L. fremontii} species richness in plot,
- \textit{L. fremontii} plant height,
- the number of inflorescences on \textit{L. fremontii} plant,
- maximum \textit{L. fremontii} percent cover in plot,
- mean \textit{L. fremontii} percent cover in plot, and
- mean date of first flowering of \textit{L. fremontii} in plot by pool.
I performed a chi square test of independence to determine whether the presence of caterpillars was related to the pool type environment (natural or constructed). The assumption of homogeneity of variances was tested and satisfied using Levene's $F$ test, $F_{(317)} = 0.54, P = 0.47$. An independent samples $t$-test was used to investigate whether caterpillar presence affects the number of viable seeds in a *L. fremontii* inflorescence. All statistical analyses for this study were conducted using SPSS version 22.
RESULTS

Pollen Supplementation

Differences among natural and constructed pool types were found for many local site characteristics, for example, plant community composition, the timing of *L. fremontii* flowering, *L. fremontii* plant height, and elevation within the pool (Appendix C). Natural vernal pools supported greater plant species richness than constructed vernal pools; \( t_{(77)} = 7.09, P < 0.001 \). Species richness per plot was greater in natural pools as compared to constructed vernal pools (Figure 4). Pool type had a significant effect on *L. fremontii* plant height; \( t_{(195)} = -4.28, P < 0.001 \). Generally, *L. fremontii* plants were taller in the constructed vernal pools than in the natural pools (Appendix C). This is consistent with the finding that constructed pools had the greatest change in plot elevation, \( t_{(77)} = -6.088, P < 0.001 \), which meant that they had deeper pool centers (\( \bar{X} = 15.79 \) cm, \( SD = 6.47 \)) as compared to the shallower natural pools (\( \bar{X} = 6.39 \) cm, \( SD = 6.39 \)).

Pollen limitation indices were calculated for each of the remaining plant pairs unaffected by caterpillar cocooning or herbivory (\( N = 79 \)), the results showed that the *L. fremontii* populations were not pollen limited. The natural pools had a mean pollen limitation index of 0.15 (\( SD = 0.25, N = 38 \)); whereas, the constructed pools had a mean pollen limitation index of 0.14 (\( SD = 0.21, N = 41 \)). In both pool types, the mean pollen limitation indices were low (PLI < 0.20).

Pollen limitation was greater in constructed pools (\( Mdn = 0.044 \)) than in natural pools (\( Mdn = 0.004 \)); however, pool type did not have a significant effect on pollen limitation (\( U = 761.5, P = 0.855 \)). Pool type did not have a significant effect on the percent of
viable *L. fremontii* seeds (*U* = 4307.0, *P* = 0.175, *N* = 197) or on the number of *L. fremontii* viable seeds (*U* = 11953.5, *P* = 0.352, *N* = 319).

In addition, the pollen supplementation treatment (open- or hand-pollinated) did not have a significant effect on the percent of viable seeds (*U* = 4769.5, *P* = 0.907, *N* = 197) or on the number of viable seeds (*U* = 12165.5, *P* = 0.466, *N* = 319) from *L. fremontii* plants in both the natural and constructed pool types.

The results of the stepwise backward regression found that maximum *L. fremontii* percent cover in plot, plot elevation within pool, and species richness in plot were the variables that best explained the dependent variable, percent of viable *L. fremontii* seeds (*R*² = 0.115, *F*(3, 193) = 8.40, *P* < 0.001). Plot elevation within pool had the strongest statistical effect on the percent of viable *L. fremontii* seeds (*β* = −0.251, *P* < 0.001), whereas the percent of viable seeds increased with decreasing plot elevation in the pools. Maximum *L. fremontii* percent cover in plot also had a negative relationship on the percent of viable *L. fremontii* seeds (*β* = −0.180, *P* = 0.009). Interestingly, species richness was positively related with percent of viable *L. fremontii* seeds (*β* = 0.145, *P* = 0.038).
Figure 4. (A) On average, natural pools on the study site supported greater species richness than constructed pools. (B) For both the natural and constructed pools, low mean pollen limitation indices indicate a general lack of pollen limitation in plants from both pool types during the study period. Error bars represent ±1 SE.
Observations of Pollinator Visitation

The mean number of pollinator visits on *L. fremontii* observed during the 10-minute observation periods was 12; the highest number of visits during a single observation period totaled 56. In total, the insect visitors observed and/or collected during the observation periods were representative of eight taxonomic families (Appendix D).

Generalist insect pollinators observed visiting *L. fremontii* included flies (Muscidae, Syrphidae, and Bombyliidae, *Conophorus* sp.), bees (Halictidae, *Halictus* sp. and *Lasioglossum* sp.), beetles and beetle larva, gnats, spiders, a wasp (Braconidae), and a skipper (Hesperiidae). No native specialist bees were observed visiting *L. fremontii* during the 31 observation periods, which was interesting because Thorp and Leong (1998) had previously described specialist bees as visitors to *Lasthenia*. However, native specialist bees (Andrenidae, *Andrena* sp., and Halictidae, *Lasioglossum* sp.) were seen visiting *Downingia bicornuta* (horned downingia).

Honey bees (Apidae, *Apis* sp.) were seen visiting the inflorescences of *Navarretia leucocephala ssp. leucocephala* (white navarretia) preferentially over *L. fremontii* and other vernal pool plant species. On several occasions, spiders were seen hiding beneath the *L. fremontii* inflorescences to capture other insect prey that visited the flowers. As described in detail above, the sunflower moth (*Homoeosoma* sp.) was also a visitor to *L. fremontii* to oviposit on the inflorescences of the plant.
Caterpillar Cocooning and Herbivory

Plants in natural and constructed pool types did not differ in the occurrence of caterpillars ($X^2_{df = 1, N = 319} = 0.152, P = 0.697$). Sixty percent of the *L. fremontii* plants collected from the natural pools were damaged by caterpillars as compared to 66 percent of the *L. fremontii* plants collected from the constructed pools.

Plants that were unaffected by caterpillars had more viable seeds than plants with observed signs of caterpillar presence (Figure 5). Caterpillar presence significantly decreased the number of viable seeds on *L. fremontii* plants by more than 50 percent, $t_{(317)} = 7.74, P < 0.001$. 
Figure 5. A comparison of the mean number of viable seeds in *L. fremontii* plants with caterpillar damage to those without caterpillar damage. The number of viable seeds was significantly less in plants with signs of caterpillar damage. Error bars represent ±1 SE.
DISCUSSION

I found no support for my hypothesis that pollen limitation in *L. fremontii* is greater in constructed versus natural vernal pools. There was no statistical difference between the pollen limitation indices sampled from constructed and natural vernal pools. The low levels of pollen limitation observed for both pool types (mean pool PLI < 0.20) suggest that pollen delivery to *L. fremontii* by pollinators was similarly effective in both the constructed and natural vernal pools during the study period. These results are similar to a pollen limitation study conducted by Faist et al. (2015) for constructed and natural vernal pools in Solano County, California. The authors did not find a significant difference between open- and hand-pollinated *L. conjugens*, and therefore concluded that the populations were not pollen limited. In comparison, Sloop et al. (2012) found no significant difference in seed set for *L. burkei* in constructed versus natural vernal pools in Sonoma County, California, though differences were seen at the pool level among pool type and across different years. It is interesting to note that in the present study, like in Faist et al. (2015) and Sloop et al. (2012), there was no significant difference in the relative seed set success found between natural and created vernal pool environments for these three *Lasthenia* species.

I did not find a significant difference between the open- and hand-pollinated treatments, which suggests that additional factors likely affect pollen limitation—not exclusively the pollination events themselves. Measurement of pollen limitation can be problematic for several reasons (Ashman et al. 2004). First, the magnitude of pollen supplementation is unknown. This is true for this study since I did not quantify the
amount of pollen transferred during the hand-pollination treatments. Second, pollen quality and rate of delivery differ between pollen-supplemented and control plants. Hand pollinations often involve pure outcross pollen, whereas natural pollinators deliver a mixture of self and outcross pollen (Thomson 2001, Ashman et al. 2004). Likewise, the hand-pollinated treatments in my study received exclusively outcross pollen from donor inflorescences. Third, under natural conditions, plants reallocate resources to seed maturity and invest in additional flower development via an adaptive timing strategy that maximizes overall plant seed set. Therefore, it stands to reason that a pollen-supplemented flower with high seed set may cause the plant to reallocate its resources differently such as reducing its resource investment towards additional flower development (Ashman et al. 2004). In my study, the degree of individual plasticity in the reallocation of resources at the plant level remains an unmeasured factor, one that likely influenced the resulting pollen limitation indices.

The natural vernal pools in this study held water for a shorter duration and dried out earlier than the constructed pools located in an area of lower elevation in the watershed. As a result of the rapid drying effect, *L. fremontii* populations located in the natural vernal pools generally bloomed earlier than those located in the constructed pools. This phenological pattern is similar to observations of Schiller et al. (2000) for *Pogogyne abramsii*. Schiller et al. (2000) concluded that delayed flowering phenology in constructed vernal pools located in San Diego County, California was likely attributed to the fact that the constructed pools held water longer following rain than the natural pools, which stymied the developmental transition from emergent aquatic into fully mature
(flowering) terrestrial *P. abramsii* plants. In my study, it turned out that the mean date of first blooming recorded for the pair of *L. fremontii* in each plot for both pool types did not have a significant effect on pollen limitation or on the percent of viable seeds produced. So, while the phenology of flowering *L. fremontii* differed among the natural and constructed pools, timing did not have an effect on seed set success in the plants examined.

Plot elevation within pool, maximum *L. fremontii* percent cover in plot, and species richness in plot all explained the percent of viable *L. fremontii* seeds produced. One explanation for the increase in the percent of viable *L. fremontii* seeds with decreasing plot elevation is abiotic constraints. As soil moisture evaporates and surface water recedes into lower elevations of the pool bottom during the drying phase, the plant’s ability to allocate resources to seed maturation is impaired. Thus, vernal pool microtopography influences patterns of annual species assembly. In a study by Emery et al. (2009), the distribution patterns of five annual plant species were examined across different microtopographical gradients in natural vernal pools in Sacramento County, California. Emery et al. (2009) found that across two growing seasons, the population boundaries of each species were consistent and shifts were observed only on the order of a few centimeters in elevation change. *Lasthenia fremontii* reached highest densities in the bottom zones of the pools. While the timing of inundation varied over the two years of the study, the elevation of population boundaries were remarkably similar in both growing seasons. Previously, others have shown that environmental factors such as hydrology, soil characteristics, and additional abiotic factors covary with elevation in
vernal pools (Lathop 1976, Holland and Dains 1990). Considering this, a plant’s position relative to the microtopography within the pool has the propensity to affect its ability to obtain nutrients and moisture from the soil (Emery et al. 2009) as well as its advertisement exposure to pollinators—factors that ultimately contribute to successful seed set.

Maximum *L. fremontii* cover in plot had a negative relationship on the percent of viable seeds. One possible explanation for this finding could be the presence of intraspecific competition in *L. fremontii* for the services of pollinators or for resources like sunlight, soil nutrients and moisture. In a study of two neotropical understory plants (*Heliconia metallica* and *Besleria melancholica*) at forest study sites in South America, Stein et al. (2013) found that differences in the relationship between reproduction and floral density largely originated from a trade-off between increasing attractiveness versus increasing competition for pollinators at high conspecific floral densities. Contrary to the perception that growth and reproduction in understory plants in neotropical forests are constricted by access to sunlight, this study found that fruit set was not directly related to canopy openness. Instead, reproductive success measured by fruit set decreased with increasing conspecific floral densities. Stein et al. (2013) point out that their findings are in contrast to those of previous studies, which show that plant reproduction usually increases with conspecific density. The authors state that one explanation for this could be the presence of intraspecific competition for pollination services or for abiotic resources. Therefore, it is reasonable to assume that the presence of intraspecific
competition in *L. fremontii* at high conspecific densities would similarly affect the ability of individual plants to maximize their seed set.

Linhart (1988) observed intraspecific competition at high densities of *Veronica peregrina* in California vernal pools. Linhart (1988) points out that stressors like elevation as well as access to soil moisture and nutrients form a complex environmental gradient, which spans across the center and edges of vernal pools. This complex gradient resulted in intraspecific competition among *V. peregrina* populations at the pool centers, where intense competition for space, moisture, and nutrients occurs during the germination and flowering phases. Ultimately, these factors affected an individual plant’s ability to attract pollinators. Linhart (1988) found that competition for resources at the periphery of vernal pools was delayed and predominantly consisted of interspecific competition among upland plant species. My finding that maximum conspecific density of *L. fremontii* had a negative effect on the percent of viable seeds is consistent with the observations of Stein et al. (2013) and Linhart (1988).

I found a positive relationship between species richness and percent viable *L. fremontii* seeds, which further supports the hypothesis presented above that intraspecific competition may have been present. Strictly speaking, species richness had a direct effect on biomass production, measured in terms of percent viable seeds, in the *L. fremontii* examined in this study. Cardinale et al. (2007) identified a similar trend in their metaanalysis performed on 44 independent experiments in which species richness had been directly manipulated. The authors found that the most diverse polycultures, or assemblages of different species, achieved nearly twice the biomass production than the
average species monoculture. This metaanalysis revealed that the net effect of plant richness on plant biomass was significantly positive. Cardinale et al. (2007) concluded that biomass production is attributed to significant effects of both the number of species and types of species in an ecosystem.

Previous metaanalyses have shown that species loss tends to reduce the efficiency by which plant communities capture biologically essential resources and convert those into new biomass. Understanding how species diversity affects the functioning of ecosystems is becoming increasingly relevant as species declines due to climate change or habitat loss are being witnessed worldwide (Cardinale et al. 2007).

In one of the largest known experimental grassland studies of its time, Hector et al. (1999) conducted experimental simulations of plant species loss and reestablishment from seed for eight field sites spanning throughout Europe, the United Kingdom, and Scandinavia. In this study the authors tracked experimental assemblages of grassland species (grasses and forbs) that varied in species richness and measured the respective above-ground biomass produced under each varying plant assembly treatment for a total of eight field sites. The authors hypothesized that biomass productivity would be lower in communities with fewer functional groups of diverse plant assemblages (or monocultures). Climate and the length of the growing season differed between the northern and southern field sites, and these environmental differences caused the northernmost sites to have the lowest biomass production due to temperature, water, and day-length abiotic constraints. Nonetheless, the results of the study confirmed that increased species richness, functional group richness, and also niche complementarity,
had significant positive effects on aboveground biomass; whereas, overall assemblages with lower species diversity were less productive on average (Hector et al. 1999). Niche complementarity is used to explain the ecological differences between species that lead to more complete utilization of resources in intact communities (Hector et al. 1999). The authors’ finding that there was a consistent average decrease in overyielding with the simulated loss of species richness provides evidence of the key underlying role of niche complementarity and positive species interactions on biomass production in plant communities.

The relationship between species diversity and increased biomass production, as shown for *L. fremontii* and demonstrated by Cardinale et al. (2007) and Hector et al. (1999), is valuable to the field of vernal pool restoration ecology, especially considering the loss of vernal pool habitat seen in recent decades throughout California. My results demonstrate the importance of species diversity in fostering seed set success in vernal pool annuals, an ecological relationship that has direct applications in vernal pool restoration and creation. Meli et al. (2014) explain that for wetland restoration projects, restoring biodiversity also supports the recovery of ecosystem services provided by wetlands. For example, wetlands support significant biotic interactions such as insect pollination services and the trophic chains linked to those services (Meli et al. 2014). Therefore, management approaches for vernal pool restoration and creation that target increasing species richness have the propensity to systematically improve biodiversity and the valuable ecological services provided by pollinators.
Understanding how plants are pollinated, and whether there are specialist or generalist pollinator relationships, must be considered in restoration efforts (Faist et al. 2015). The mutualistic interaction of native solitary bees and their vernal pool annual host plants is widely recognized as an important ecological service provided by specialist pollinators (Thorp 1990, Thorp and Leong 1998). Contrary to my expectation, I observed that *L. fremontii* was visited entirely by generalist insects such as flies, bee flies, gnats and beetles. Possible explanations for this observation could be attributed to floral morphology, pollinator abundance, characteristics and scale of conditions across the landscape, and/or past disturbances at the site.

The showy, wide, floral display and large platform head of disk flowers, which are characteristic of the Asteraceae, likely influenced the plant’s advertisement success for pollination services by generalist, opportunistic insect foragers. Thorp and Leong (1998) described visitors to the major, showy vernal pool flower genera to be diverse and typically containing many species of generalist bees, flies, and beetles. The authors point out that among vernal pool endemics, species such as *Downingia* sp. attract relatively fewer visitors due to its specialized flower form, whereas *Lasthenia* sp. attracts the greatest diversity of visitors owing to its less-specialized floral morphology. I observed a similar pollinator foraging pattern at my study site. During the observation periods, specialist native bees were observed visiting *Downingia* sp. preferentially over *L. fremontii*. The foraging behavior of the specialist bees at my study site included flying near or around *L. fremontii* but not landing on its inflorescences.
Faist et al. (2015) found that local pollinator abundance and the floral morphology of *L. conjugens* facilitated its visitation by a suite of different pollinators, including gnats, beetles, and flies in constructed vernal pools in Solano County, California. In this study, Faist et al. (2015) conducted observations to assess the number and type of pollinators visiting *L. conjugens* and subsequently dissected a set of *L. conjugens* flower heads to measure viable seed production. The authors observed a stark contrast in the pollinator community between the two pool types. There was a high abundance of gnats and low abundance of specialist native bees observed at the constructed pools. Conversely, at the natural pools there was a low abundance of gnats but a high abundance of specialist native bees. Interestingly, the high abundance of gnats observed at the constructed pools combined with the high number of viable seeds found in *L. conjugens* in those pools led the authors to conclude that the gnats may be acting as surrogate pollinators of *L. conjugens* in the constructed vernal pools.

My data analysis failed to detect pollen limitation in *L. fremontii*, which is consistent with the explanation posed by Faist et al. (2015) who suggest that it may not be strictly necessary that the “correct” pollinators be introduced in conjunction with vegetation in vernal pool restoration projects because surrogate pollinators might be just as effective. In concert with the findings of Faist et al. (2015), my study contributes to the field of applied restoration ecology by drawing attention to the fact that *Lasthenia* plays a role as a generalist plant species whose seed set success is influenced by plant community composition and the abundance of opportunistic, generalist insect foragers.
The same morphological features that influenced visitation to *L. fremontii* by generalist insects may also partly explain why *L. fremontii* was susceptible to infestation by the sunflower moth (*Homoeosoma* sp.). The sunflower moth (*Homoeosoma electellum*) has been previously described as the most widespread and economically damaging herbivore to sunflowers across North America (Schultz 1978, Charlet et al. 1997), since it attacks both agricultural and wild sunflowers by feeding on the florets and seeds in the flower head (Rogers 1978). In a field study at the Stone Lakes National Wildlife Refuge in Yolo County, California, Chen and Welter (2002) compared the abundance of *H. electellum* larva on domesticated or agricultural sunflowers (*Helianthus annuus* var. *macrocarpus*) and wild sunflowers (*H. annuus* var. *annuus*). The authors found higher larval densities on agricultural sunflowers (a magnitude of 200 times greater) than on the wild sunflowers. The authors noted that differences in flower size and plant flowering phenology between agricultural and wild sunflowers may influence the trophic interactions between *H. electellum* larva and its natural predators.

Larval age distribution of *H. electellum* varied more with flower age in wild sunflowers than when tracked with agricultural flower age. The authors suggest possible explanations for this pattern may include that the small size and pace of development of wild sunflowers may cause flower tissue to be exhausted and/or unpalatable sooner, which forces the *H. electellum* larvae to migrate from older flowers to younger ones to complete development. This finding is consistent with my observations of *Homoeosoma* sp. caterpillars occupying both newly opened and older *L. fremontii* flowers as well as climbing the stems of unaffected plants to feed on the open flowers. Chen and Welter
point out that the *H. ellectellum* larva behavior of relocating to a different plant host may increase its exposure and susceptibility to predators, which in turn may serve as an important regulator of this herbivore in wild sunflower populations.

Chen and Welter (2002) investigated the parasitoid activity on *H. ellectellum* and found that while *H. ellectellum* larva populations were consistently more abundant on agricultural sunflowers, native parasitoid abundance was much lower on agricultural sunflowers than on wild sunflowers. Higher levels of disturbance in agricultural habitats, including post-harvest tilling, and larger flower size may be causes for why natural parasitoids were observed to be poor colonizers of agricultural sunflowers (Chen and Welter 2002). The authors also explained that the parasitism success rate of individual parasitoids was lower for agricultural sunflowers as compared to the wild sunflowers. To the best of my knowledge, *L. fremontii* has yet to be described in the literature as a host plant of *Homoeosoma* sp., therefore the role of natural parasitoids in regulating *H. ellectellum* populations may be worth examining in a future study to determine the abundance and effectiveness of natural parasitoids in regulating *Homoeosoma* sp. caterpillar herbivory on *L. fremontii* in vernal pools.

The loss of viable seeds due to herbivory and how this affects the overall seasonal contribution of *L. fremontii* to the seed bank is difficult to assess and quantify. Few studies have examined the persistence of seeds in vernal pool seed banks, yet a study by Faist et al. (2013) provides evidence that suggests native seeds can remain dormant but viable for decades in the seed bank. Given the extraordinary endurance of vernal pool annuals, a decline in viable seed bank stores deposited over one season may not affect a
species’ persistence in the short term; however, it stands to reason that the widespread destruction to L. fremontii caused by Homoeosoma sp. caterpillar herbivory that was observed in this study highlights the need for additional research and monitoring to determine if continued herbivory on L. fremontii could jeopardize its long term persistence.

The placement of vernal pool restoration and construction projects near large-scale commercial sunflower crops may increase their exposure and susceptibility to invasion by the sunflower moth (Homoeosoma sp.). Likewise, this proximity between domesticated and wild species in the Asteraceae may further increase the resiliency of Homoeosoma sp. infestations due to the abundance of host plants. As a result, this invasive herbivore has the propensity to cause ecological damage to our fragile vernal pool ecosystems in California. Further research is needed to understand the climatic and environmental conditions that may be responsible for cueing Homoeosoma sp. infestations. Future research efforts should focus on assessing the impacts of Homoeosoma sp. on non-cultivated Asteraceae populations where found in vernal pools, open grasslands, and roadside areas in the Central Valley.
CONCLUSION

The preservation and restoration of vernal pools is of great interest as they provide critical habitats for the maintenance of biological diversity (Faist et al. 2013) and essential ecological services such as pollination (Thorp and Leong 1998). Contrary to my hypothesis, the L. fremontii populations examined in the natural and constructed pools were not pollen limited. Consistent with observations previously shown for two other Lasthenia species endemic to vernal pools (Faist et al. 2015, Sloop et al. 2012), in this study there was no significant difference found between the relative seed set success of L. fremontii between natural and constructed vernal pools.

Plant species richness in vernal pools was positively associated with the percent viable L. fremontii seeds in the constructed and natural pools; while, plot elevation and maximum percent cover of L. fremontii had negative effects on the percent of viable seeds. The relationship between species diversity and increased biomass production, as shown for L. fremontii, and previously demonstrated by others (Cardinale et al. 2007, Hector et al. 1999), is valuable to the field of vernal pool restoration ecology, especially considering the loss of vernal pool habitat seen in recent decades throughout California. Restoration projects that restore plant species diversity thereby enhance niche complementarity and positive species interactions, ecological functions that play a key role in the maintenance of biomass production and healthy plant communities (Hector et al 1999).

Similar to the observations of Faist et al. (2015) for L. conjugens in constructed vernal pools, visitors observed on L. fremontii were comprised entirely of generalist
insects and not specialist native bees. The widespread infestation of the sunflower moth 
(Homoeosoma sp.) on L. fremontii resulted in a loss of 39 percent of the plants under 
investigation in this study, a finding that may shed new light on a host plant species that 
was formerly undocumented as one utilized by the sunflower moth.
APPENDICES
Appendix A. Photographs of sunflower moth (*Homoeosoma* sp.) caterpillars observed in plots within the natural and constructed vernal pools.
Appendix B. Photographs showing healthy *L. fremontii* inflorescences compared to ones affected by sunflower moth (*Homoeosoma* sp.) caterpillars.
Appendix C. Characteristics of *L. fremontii* populations in the 20 vernal pools.

<table>
<thead>
<tr>
<th>Pool Type</th>
<th>Pool</th>
<th>Mean percent cover of <em>L. fremontii</em> (%)</th>
<th>Mean date of first flowering in plots by pool (2014)</th>
<th>Mean plot elevation (cm)</th>
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Appendix D. Pollinator visitors identified by observation or collection from the study site.

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<th>Insect description</th>
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<th>Genus</th>
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<td>Syrphidae</td>
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<td>LasioGLOSSum</td>
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<td>Braconidae</td>
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<td>leucocephala)</td>
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LITERATURE CITED


Sloop, C.M., K. Gilmore, H. Brown, and N.E. Rank. 2012. An investigation of the reproductive ecology and seed bank dynamics of Burke’s goldfields (Lasthenia burkei), Sonoma sunshine (Blemnosperma bakeri), and Sebastopol meadowfoam (Limnanthes vinculans) in natural and constructed vernal pools. Final Project Report E-2-P-35. California Department of Fish and Game U.S. Fish and Wildlife Service: Endangered Species Act (Section 6) Grant-in-Aid Program. Prepared for Cherilyn Burton, California Department of Fish and Game, Habitat Conservation Division, Sacramento, CA, USA.


