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Ecological factors suitable for the endangered Lasthenia conjugens (Asteraceae)

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ECOLOGICAL FACTORS SUITABLE FOR THE ENDANGERED

LASTHENIA CONJUGENS (ASTERACEAE)

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by

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ABSTRACT

ECOLOGICAL FACTORS SUITABLE FOR THE ENDANGERED *LASTHENIA CONJUGENS* (ASTERACEAE)

by Danielle N. Tannourji

For future introduction efforts, various ecological factors supporting the growth of the federally endangered *Lasthenia conjugens* E. Greene (Contra Costa goldfields; Asteraceae) were examined in seven vernal pool complexes at Fort Ord near Monterey, California. Over a two-year period, *L. conjugens* abundance was measured in addition to several descriptors of the abiotic and biotic environment, including seasonal inundation, aquatic and edaphic parameters, plant diversity, and pig disturbance. Linear regression was used to analyze percent cover of *L. conjugens* in relation to the abiotic and biotic factors examined. Those factors that related to *L. conjugens* abundance were then tested for differences across complexes with and without *L. conjugens*. Inundation, water temperature, water pH, water holding capacity, and native species richness were positively related to *L. conjugens* abundance. Of these factors, water temperature, water pH, and native species richness differed significantly among complexes with and without *L. conjugens*. The data suggest that *L. conjugens* thrives in pools with longer inundation regimes, warmer waters, neutral water pH, and greater native species richness. The four complexes that lack this rare endemic appear to fall out of the mean ecological range for several of the factors related to *L. conjugens* cover and, therefore, would be unsuitable for introduction efforts of *L. conjugens*.

TABLE OF CONTENTS

TABLE OF CONTENTS, Continued

LIST OF FIGURES

LIST OF FIGURES, Continued

LIST OF TABLES

LIST OF ABBREVIATIONS

ANCOVA	analysis of covariance
ANOVA	analysis of variance
AR	Addington Road
BLM	U.S. Bureau of Land Management
BV	Butterfly Valley
°C	degrees Celsius
CB	Crescent Bluffs
CDEC	California Data Exchange Center
cm	centimeter
g	gram
h	hour
ha	hectare
km	kilometer
L	liter
m	meter
MANOVA	multivariate analysis of variance
masl	meters above sea level
MGF	Machine Gun Flats
min	minute
mL	milliliter

mm	millimeter
mol	mole
mS	millisiemens
MV	Mary's Valley
NRMA	Natural Resources Management Area
OR	Oak Ridge
ppm	parts per million
RMANOVA	repeated measures analysis of variance
SE	standard error
TR 17	Trail 17
USACE	U.S. Army Corps of Engineers
USDA	U.S. Department of Agriculture
USFWS	U.S. Fish and Wildlife Service

INTRODUCTION

One of the research goals in ecology today is to understand the mechanisms that influence biodiversity. Abiotic and biotic factors such as temperature, rainfall, and grazing are common mechanisms that affect the world's landscapes and the species that inhabit them (Marty 2005). Monitoring these effects on plant and animal communities can reveal the shifts and trends in biodiversity we see today. Understanding these trends can lead to rare species recovery, improved conservation measures, and focused land management efforts in the remaining preserved areas across the globe.

Vernal pools are one of many rare communities found in Mediterranean climate regions that support rich biodiversity. These ephemeral freshwater wetlands are characterized as shallow flooded depressions underlain by an impermeable substrate, often hardpan or claypan (Stone 1990). With the cool wet winters and hot dry summers typical of a Mediterranean climate, pools inundate in the winter, dry down in the spring as precipitation decreases, and dry out in the summer and fall (Keeley and Zedler 1998). Vegetation consists predominately of distinct annual species that complete their life cycle during the spring months while soil moisture persists (Barbour et al. 2003). Seasonal conditions serve as important selective pressures in shaping the evolution of specialized biota with distinct distribution patterns and localized population dynamics. For example, California vernal pools harbor over 70 endemic plant and invertebrate species (Baskin 1994) across 17 vernal pool regions (Keeler-Wolf et al. 1998), making this community one of the state's most unique ecosystems.

Vernal pools were once a common part of the landscapes occurring along the west coasts of North and South America, in South Africa, the Mediterranean Basin, and in southern Australia (Keeley and Zedler 1998). Currently, these wetlands are disappearing rapidly due to habitat destruction and fragmentation caused by anthropogenic land use (Holland 1986, 1998; Keeley and Zedler 1998). The vernal pools found along the west coast of North America have the greatest diversity as well as the highest level of habitat loss of these seasonal wetlands found worldwide (Barbour et al. 2003). Approximately 90% of California vernal pool plants are native and ~55% have distributions limited to the state (Barbour et al. 2003). Although it is not known exactly how much vernal pool habitat has been lost in California over the last 200 yr, estimates based on soil maps and aerial imagery conclude a loss of ~60-90% (Holland 1986; Barbour et al. 2003). As a result, populations of several California vernal pool species have declined and are now listed as rare, threatened, or endangered under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1997; Keeler-Wolf et al. 1998). This action has prompted a new conservation movement by local, state, and federal organizations to restore and preserve the remaining vernal pool habitats left that support a high percentage of California's biodiversity (Holland and Jain 1977; Holland 1998).

An important aspect of these restoration efforts is to understand the relationships between rare endemics and their abiotic environments. Detailed studies have concluded that vernal pool plants are dependent on local climatic patterns and, therefore, are subject to annual hydrologic fluctuations (Hanes and Stromberg 1998). Yearly variations in the duration of the growing season, germination cues, and overall species abundance and composition between pools and across different sites have been reported (Holland and Jain 1984; Barbour et al. 2003). For instance, a species may germinate readily under a range of soil moisture regimes noted across its distribution, but studies have shown differentiation in response to local environmental conditions such that seeds from one region may not germinate or survive well if introduced to another region (Linhart 1988; Collinge et al. 2003). Thus, studying how climate affects inundation at multiple locations can provide new insights into population differences and, ultimately, restorative techniques at the local level.

Determining edaphic factors, such as soil pH and salinity, is also pertinent to conservation strategies. The temporary nature of vernal pool habitats creates unusual soil conditions resulting in localized species richness and ecological tolerances as well as restricted dispersal (Holland and Dains 1990; Rajakaruna and Bohm 1999). For example, low soil salinity has been shown to be correlated with increased population size in some vernal pool species, including the federally endangered *Lasthenia conjugens* E. Greene (Contra Costa goldfields; Asteraceae) (Dains 1995). Variations in soil type, texture, and depth to the impermeable hardpan also influence species abundance observed in vernal pool complexes (Holland and Dains 1990). Therefore, knowing which factors or combinations thereof correlate with successful population growth will play a leading role in defining introduction efforts for rare and listed species.

Management of biotic factors, such as grazing, is another crucial facet in conservation planning. Grazing by native herbivores is known to maintain species diversity and reproductive fitness in many communities (Hayes and Holl 2003; Marty

2005). However, many of these native grazers have been extirpated and replaced with non-native species such as cattle or feral pigs. Disturbance from these introduced species has negatively affected ecological systems due to poorly controlled grazing. Recent field studies in Sacramento Valley vernal pools (Marty 2005) and in coastal California grasslands (Hayes and Holl 2003) have revealed that livestock can serve as an ecological equivalent to native herbivores and maintain diversity for vernal pool endemics if managed correctly. Studies on feral pig disturbances in vernal pool communities are lacking, but manipulative experiments (*i.e.*, pig enclosures) in grasslands have resulted in negative effects on ecosystem function and rare species composition (Tierney and Cushman 2006). Thus, further investigation of pig presence will also contribute to restorative policies for endangered species such as *L. conjugens* that are vulnerable to such disturbances.

As one of several endemics listed as endangered under the Endangered Species Act, *L. conjugens* is a small (< 40 cm tall), showy annual herb, known from vernal pools as well as vernal swales and mesic flats in the Central Valley and coastal northern California (USFWS 2005a). Historically, it was observed in alkaline depressions of the eastern San Francisco Bay and reported from seven vernal pool regions in California: Mendocino, Santa Rosa, Lake-Napa, Solano-Colusa, Livermore, Central Coast, and Santa Barbara (Keeler-Wolf et al. 1998). In addition, Ornduff (1966) located 13 sites outside of these vernal pool regions in ephemeral mesic habitats. Currently, this rare plant persists from Mendocino to Monterey in only 24 of the 34 occurrences recorded between 1884 and 2005 (USFWS 2005a).

As a result of *L. conjugens* decline, conservation measures have been implemented over the past decade. The USFWS listed *L. conjugens* as endangered in 1997 under the Endangered Species Act. Efforts continued in 2003 when USFWS designated ~420,000 ha of critical habitat for *L. conjugens* and 14 other vernal pool specialists throughout California and southern Oregon (USFWS 2003). This total area was reduced to ~350,000 ha in 2005 due to economic reasons, but still spans the current range of *L. conjugens* distribution (USFWS 2005b). Moreover, six populations occur on public lands that will be preserved in perpetuity: one at San Francisco Bay Wildlife Refuge (Alameda County; USFWS), one at Travis Air Force Base (Solano County; U.S. Department of Defense), and four at the former Fort Ord (Monterey County; U.S. Bureau of Land Management [BLM]).

Studies conducted in Solano and Napa Counties have resulted in findings specific to the northern portions of the species' range (Collinge et al. 2003) where climatic and edaphic conditions differ from those of the southern populations on the Central Coast. The studies found that northern inland populations were found in pools with longer inundation regimes, greater water depths, neutral soil pH, and a later growing season. Therefore, to further understand ecological factors supporting this rare endemic in its southernmost range and provide new restoration measures at the local level, three populations of the federally endangered *L. conjugens* located at Fort Ord, Monterey County, California were studied over a two-year period. I investigated various abiotic and biotic factors at the three vernal pool complexes that harbor *L. conjugens* in addition to four vernal pool complexes within a 5-km radius that lacked this rare endemic.

Abiotic factors such as rainfall, water depth, water temperature, inundation regime, soil pH, and nitrogen availability were studied at each complex. Biotic factors including native and non-native species richness, percent cover, and feral pig disturbances were also quantified.

Specifically, the presence and absence of *L. conjugens* in relation to six sets of factors in both the abiotic and biotic environment were explored: (1) inundation, (2) aquatic environment, (3) pool area, (4) soil conditions, (5) plant diversity, and (6) pig disturbance. The distribution and physical traits of *L. conjugens* were also monitored.

By examining these subsets of ecological parameters affecting *L. conjugens* populations in the natural environment and comparing them to similar vernal pool habitats within the vicinity, this study provides new insights into the natural history of *L. conjugens* and guides future restoration efforts for population recovery in its southernmost range.

STUDY SITE

In 1991, the U.S. Department of the Army was ordered to close and clean up Fort Ord, which is located ~10 km northeast of Seaside along the central coast of Monterey County, California (Latitude 36°38'3.77"N; Longitude 121°44'56.47"W) (Fig. 1) (U.S. Army Corps of Engineers [USACE] 1992). This federal action required approval from the USFWS for possible take of federally-listed species and their critical habitat. As a result, the USFWS issued a Biological Opinion in 1993 outlining the potential impacts to federally-listed species and required the U.S. Department of the Army to implement a

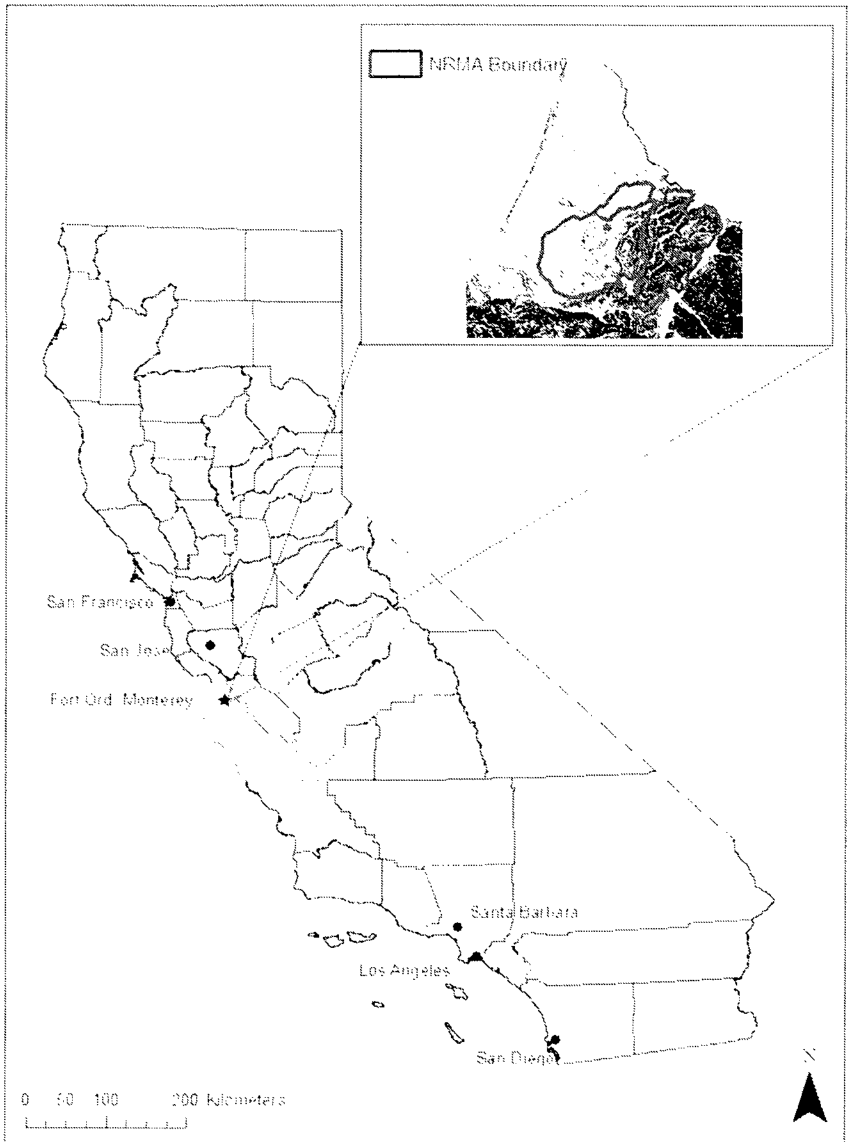

FIG. 1. Site location of BLM lands on the former Fort Ord Army Base in Monterey County, CA with a caption showing the Natural Resources Management Area (NRMA) boundary over a hill-shade map. The darker the color shade, the higher the elevation.

habitat management plan. By 1997, the habitat management plan was revised and approved by the USFWS.

The mission of this plan is to preserve and restore habitat for federally-listed species found on the base and impacted by the proposed closure and reuse activities, including land transfers and urban development. The land is now operated by the BLM and referred to as the Natural Resources Management Area (NRMA) of the former Fort Ord (USACE 1992). The NRMA is characterized by 6,070 ha located ~14 km north of Monterey and ~18 km west of Salinas and is dominated by low-lying hills that range in elevation from ~120 to 165 masl (USACE 1992). The climate of this region is Mediterranean with an average annual rainfall of ~50 cm, 95% of which falls from October to April (USACE 1997). Average winter and summer temperatures range from ~8.3 to 15.6 °C, respectively (USACE 1997).

The northwestern area of the NRMA consists of 12 vernal pool complexes within a 5 km radius. Seven of these complexes were selected for this two-year study based on their similar species composition, geologic formation, and inundation regime (Fig. 2). All vernal pool complexes at the study site occur within foothill/valley grasslands surrounded by maritime chaparral and/or coast live oak woodland (Sawyer and Keeler-Wolf 1995). All seven complexes occur over the Paso Robles geologic formation (USACE 1992) with the upper surfaces dominated by older eolian sand deposits of the Pleistocene epoch (L. Rosenberg, unpublished data, 2001). Three soil types are known from these claypan depressions: Antioch sandy loam, Arnold-Santa Ynez Complex, and Oceano loamy sand (U.S. Department of Agriculture [USDA] 1961).

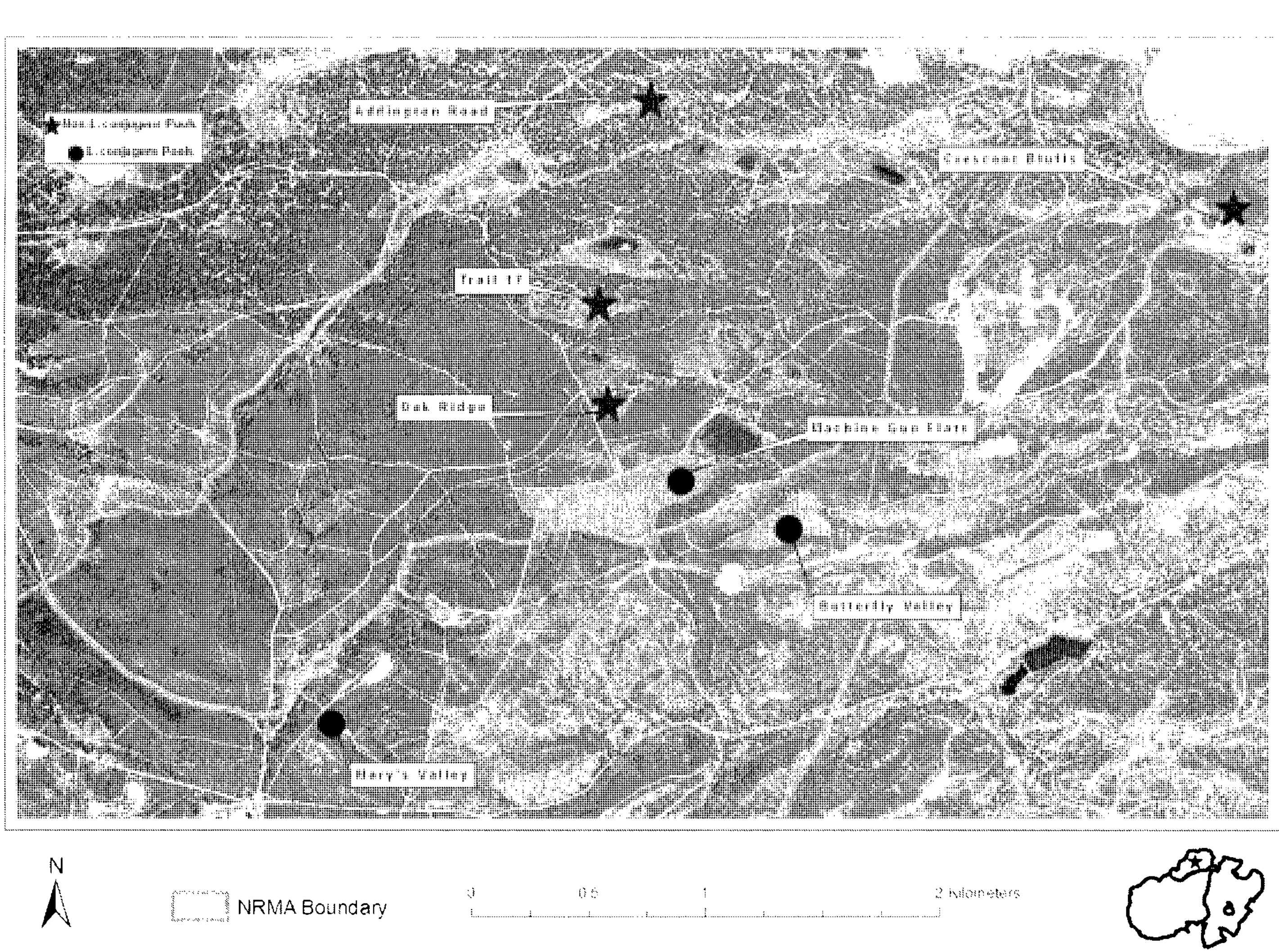

FIG. 2. Seven vernal pool complexes located within and adjacent to the northwestern portion of the NRMA were sampled over the two-year study on lands of the former Fort Ord, Monterey County, CA.

Historically, all sites have been disturbed by army training activities such as off-road vehicle use, road maintenance, gun-firing, and fox-hole preparation (USACE 1992). These disturbances were predominantly restricted to upland areas with little impact to the pool basins. Presently, feral pigs are the main disturbance agent in the NRMA and have become a central target in BLM's invasive species removal project.

Of the seven complexes used in this study, three, known as Butterfly Valley, Mary's Valley, and Machine Gun Flats, harbor *L. conjugens* (Fig. 2). Butterfly Valley consists of six vernal pools, all of which are characterized by intense soil disturbances (*e.g.*, excavation, uprooting, and burrowing) caused by pig activity. Four of the six pools are known to harbor *L. conjugens*. Mary's Valley contains eight vernal pools, six of which are known to harbor the endangered species and consist of low levels of pig disturbance. Machine Gun Flats is made up of six vernal pools with low pig disturbance, three of which are known to harbor *L. conjugens* (USFWS 2005a). In summary, 13 out of 20 pools harbor *L. conjugens* within these three complexes.

The complexes described above are regarded by the BLM as environmentally sensitive habitat areas that support, not only *L. conjugens*, but also several other special-status species: *Allium hickmanii* Eastw. (Hickman's onion; Liliaceae), *Plagiobothrys chorisianus* var. *hickmanii* E. Greene (Hickman's popcorn flower; Boraginaceae), *Calandrinia breweri* S. Watson (Brewer's red maids; Portulacaceae), and *Linderiella occidentalis* Dodds (California fairy shrimp; Chirocephalidae) (USACE 1997).

In addition, a variety of native vernal pool forbs and grasses are known from the three complexes with *Eryngium armatum* S. Watson (prickly eryngo; Apiaceae), *Plagiobothrys tenellus* Nutt. (slender popcorn flower; Boraginaceae), *Eleocharis macrostachya* Britton (pale spike-rush; Cyperaceae), and *L. conjugens* as dominant species. Uncommon soil types also exist at the three sites: Antioch sandy loam soils occur at Butterfly Valley, and Arnold-Santa Ynez Complex soils occur at Mary's Valley and Machine Gun Flats (USDA 1961).

The remaining four vernal pool complexes examined in this study do not support *L. conjugens* populations, but do harbor similar vernal pool plant associates observed within the three *L. conjugens* complexes described above. The four alternate complexes include Addington Road, Crescent Bluffs, Trail 17, and Oak Ridge (Fig. 2). Addington Road is made up of three pools dominated by *E. armatum* and *P. tenellus* on Oceano loamy sand with no pig disturbances. Crescent Bluffs has two pools dominated by *P. tenellus* and *E. armatum* on Oceano loamy sand with no pig disturbances, but is characterized by past army training disturbances. Trail 17 has two pools dominated by *E. macrostachya*, *E. armatum,* and *P. tenellus* on Arnold-Santa Ynez Complex soils with no pig disturbances, but is also marked by past army training disturbances. Oak Ridge is characterized by one pool dominated by *P. tenellus* and *E. armatum* on Antioch sandy loam with low levels of pig disturbance. These four complexes, collectively referenced herein as the four alternate complexes, were chosen based on the presence of temporary inundation during the 2006-07 wet season and similar vernal pool composition in the 2006-07 blooming season.

MATERIALS AND METHODS

Butterfly Valley, Mary's Valley, and Machine Gun Flats were examined for both abiotic and biotic parameters between October 2006 and May 2008. Inundation, aquatic environment, and pool area parameters were documented during the wet season (October to March). Soil and flora analyses were conducted during the dry spring blooming period (April to June). The four alternate complexes were examined for the same parameters between October 2007 and May 2008. Below are descriptions of each field method used at the seven vernal pool complexes to comparatively examine ecological parameters and establish trends within pools that harbor *L. conjugens*.

Inundation and Precipitation

Because inundation can affect establishment and growth of plant species in vernal pools, the inundation period was monitored at each complex. Each pool was visited ~24 h after a major rain event ($\geq$2.5 cm) to identify the first ponding event of the wet season. From that date, each pool was monitored weekly for presence of water until dry conditions persisted. These data were used to determine the total and maximum inundation periods, as well as the number of dry-down events for each pool in a given wet season (Marty 2005).

The average and maximum pool depths were recorded for each pool each week if water was present during the 2007-08 wet season. Depth measurements were taken every other meter starting at 0 m along a fixed transect line along the pool's central axis. Measurements were taken in cm using a ruler. These measurements were repeated for those pools that ponded multiple times during the rainy season.

Daily precipitation and temperature were collected from the California Department of Water Resources weather station located within the NRMA. This station is at an elevation of ~150 masl and within ~0.25 to 5 km of the pool complexes. Daily records from October 2006 to May 2008 were accessed online through the California Data Exchange Center (CDEC) managed by the California Department of Water Resources (CDEC 2008).

Aquatic Environment

Four abiotic factors known to affect the aquatic environment and plant establishment within vernal pools were measured during the two wet seasons: water temperature, dissolved oxygen, electrical conductivity, and water pH. Each factor was measured in the field at the maximum ponding period (*i.e.*, the period during the wet season when a pool has reached its greatest volume) using an automated, multi-parameter water quality meter (YSI 55 Dissolved Oxygen Meter, Enviro-Tech Services Company, Martinez, CA).

Additional repeated measurements for water temperature and pH were conducted every seven days during the 2007-08 wet season to test for weekly changes among pool complexes. During the measurements, water temperature was inspected using a digital pocket thermometer in °C (Miller Thermometer Co., Hartford, MI). Water pH was examined using pHydrion dip sticks (Sigma-Aldrich, Inc., St. Louis, MO) ranging in pH from 0 to 13.

Pool Area

The overall size of a pool may affect abiotic conditions and plant establishment; therefore, pool areas were measured within the seven complexes during each wet season. At maximum ponding, the total surface area of each pool was estimated by measuring the distance of the existing water's edge from a defined transect line set parallel to one side of the pool (lengthwise). At every 1.5 m, distances to the water's edge were measured to the nearest 0.1 m for both sides of the pool. These distances were then converted into an *x*- and *y*-coordinate system, where *x*-coordinates were the 1.5 m increments defined along the transect line and the *y*-coordinates were the set of distances measured perpendicular from the transect line to the existing water's edge on both sides of the pool. These *x*- and *y*-coordinates were then entered into a computer-aided drafting and manufacturing software (MasterCam X2 Student Version, CNC Inc., Tolland, CT) to calculate pool areas.

Soil Conditions

Soil conditions and nutrient properties that may also affect plant establishment and growth were characterized for each of the pool complexes. Soil samples were collected in the field to analyze plant-available nitrogen, pH, electrical conductivity, and salinity. To minimize damage to each vernal pool and the existing *L. conjugens* populations while assessing soil conditions in the field, only one soil core was sampled near the center of each pool where common vernal pool vegetation occurred. Each soil core was dug down to 100 cm, but only 100 g of the first 25 cm of the topsoil was collected for laboratory soil analyses.

For each pool, a random sample of 10 g of the collected soil was analyzed for nitrogen availability through services of the ANR Analytical Laboratories at UC Davis, California. Soil pH was examined using a 2:1 solution to soil ratio both with deionized water and calcium chloride solutions. Approximately 10 g of soil were added to 20 mL deionized water or 20 mL 0.01 mol/L calcium chloride solution. The solutions were stirred four times over a 30 min period and allowed to stand for 1 h (Kalra and Maynard 1991). After the soil solution had settled, pH was measured using a multiple parameter meter (VWR, Inc., West Chester, PA). Electrical conductivity and salinity were determined using a 5:1 water to soil ratio with 15 g of soil per pool. Each sample was shaken for 1 h and then filtered before testing the two parameters using a multiple parameter meter (VWR, Inc., West Chester, PA) as detailed in the respective protocols by Kalra and Maynard (1991).

Approximately 5 g of soil from a subsample of pools per complex was used to explore the soil water holding capacity for each complex using the weight computation protocol outlined in Folk (1980). In addition, 10 g of soil collected from the same subsample of pools was used analyzed for sand, silt, and clay percentages using the pipette analysis protocol in Folk (1980).

Existing soils mapped by USDA (1961) were verified in the field at each complex during the spring sampling season of 2007. Field methods followed the USDA guidelines for identifying hydric soils (Hurt et al. 1996). Soil type was confirmed by analyzing color and texture in the field using the Munsell soil chart and the USACE texture-by-feel method (Environmental Laboratory 1987).

Lastly, soil moisture was measured in the field during the spring sampling season of 2008. Volumetric soil water content was measured at five quadrat locations in each pool using a time domain reflectometry probe (Field Scout TDR 200, Spectrum Technologies, Plainfield, IL) equipped with 20 cm rods.

Plant Diversity

To assess differences in plant species diversity and richness, plant cover and composition were estimated in each of the pools. Measurements were made twice during each spring season after pools dried and flowers were in bloom to capture early (April-May) and late (May-June) blooming species within the complexes. Data was collected using five 20 × 50 cm quadrats randomly positioned in each pool. Each plant species within the quadrat was given a Braun-Blanquet (1965) cover class value. The Braun-Blanquet rating system divides percent cover into six classes: 1) <1%; 2) 1-5%; 3) 6-25%; 4) 26-50%; 5) 51-75%; and 6) >75%. Each cover class was converted into midpoint cover values to estimate relative cover (Marty 2005). Species richness was also computed by counting the total number of native and non-native species per quadrat.

Lasthenia conjugens Pool Distribution

To determine if *L. conjugens* occurred within a specific pool zone (*e.g.*, the deepest part of the pool or the edges of the pool), point-intercept transects were conducted in a random sub-sample of pools that support *L. conjugens* at Butterfly Valley and Mary's Valley in 2008. A 5 m transect was stretched in a random direction across the center of each pool and all plant species touching the line were recorded. Two zones (*i.e.*, center and margin) were subjectively chosen by observing the micro-topography of the pool along the 5 m transect. Percent cover of *L. conjugens* was then calculated in each of the two sections within the pool and analyzed for differences in occurrence and cover.

Lasthenia conjugens Floral and Vegetative Traits

To capture the variability in *L. conjugens* floral and vegetative traits within the three complexes of the NRMA, a series of traits were measured during the two spring sampling seasons. These traits included plant height, inflorescence diameter, disk diameter, and ray flower length. Using a digital caliper, these four traits were measured to the nearest 0.01 mm for three randomly chosen plants per quadrat. In addition, the number of ray flowers was counted for each of the three individuals per quadrat.

Pig Disturbance

To determine differences in plant species diversity and abundance in relation to pig presence, soil disturbance was estimated during the early spring sampling of 2008 within each complex. Pig disturbance, such as soil uprooting or excavation, observed in each quadrat was estimated using the same Braun-Blanquet rating system as described above. In addition, total pig disturbance within each pool basin was classified into four levels: high (>50%), moderate (25-50%), low disturbance (<25%), and none (0%).

Data Analyses

Both abiotic and biotic parameters were first analyzed with Pearson's correlations to test for relatedness with *L. conjugens* percent cover. The factors that resulted in significant correlations were then analyzed using linear regression. Multivariate analysis of variance (MANOVA) was conducted to test for differences among pools with and without *L. conjugens*. Significant differences identified with the MANOVA were then analyzed using nested analysis of variance (ANOVA) to test for differences between pools with and without *L. conjugens* within the three complexes that harbored *L. conjugens*. Due to the inadequate number of *L. conjugens* pools at the four alternate complexes, nested ANOVA could not be used to test across all seven complexes. The factors that resulted in significant differences in the nested ANOVAs were then analyzed using *t*-tests to compare the data from only *L. conjugens* pools of the three *L. conjugens* complexes to all pools at the four alternate complexes. Factors that did not result in significant differences in the nested ANOVA were analyzed using a *t*-test to compare data from all pools of the three *L. conjugens* complexes to all pools of the four alternate complexes.

Analysis of covariance (ANCOVA) was conducted to test for year-to-year differences in all parameters at the three *L. conjugens* complexes (data collection at the four alternate complexes was conducted for only one year). Repeated measures ANOVA (RMANOVA) was conducted for water depth, water temperature, water pH for estimates taken during the wet season of 2007-08. A *t*-test was used to test for differences in *L. conjugens* percent cover between the two pool zones.

All analyses were conducted using the statistical software SYSTAT (v. 10.0 SPSS, Inc., San José, CA). The level of significance for all tests was $\alpha = 0.05$. The homogeneity of variance within all tests was determined using Levene's test, while plots of the residuals were examined to evaluate the assumption of normality. Data that did not conform to a normal distribution, including ammonium content, water holding capacity, soil moisture, sand and silt percentage, non-native cover, and bare ground cover, were transformed using sine transformation. Log, arcsine, and square root transformations were used for data on inundation regime, nitrate content, and non-native species richness, respectively. Although tests were performed using transformed data, means and standard errors for the untransformed data are reported and illustrated. The Kolmogorov-Smirnov test was then conducted on all transformed variables to ensure that the assumptions of normality were met.

RESULTS

Climate

In 2006-07, precipitation totaled 21.7 cm and fell consistently throughout the wet season, although December and February were the wettest months receiving ~6.5 cm each (Fig. 3). In 2007-08, rainfall totaled 29.6 cm, with January receiving ~12 cm and April receiving ~6.4 cm. Average daily temperatures were similar across the years, ranging from 8.3 to 13.3 °C in 2006-07 and 8.9 to 14.4 °C in 2007-08 (Fig. 4).

Lasthenia conjugens

Lasthenia conjugens percent cover was significantly different between the three complexes in April (MANOVA, $F_{2,\,129} = 17.87$, $P < 0.0001$) and May ($F_{2,\,129} = 11.01$, $P < 0.0001$). Percent cover at Butterfly Valley (13.6 ± 1.5 %) was significantly higher than at Mary's Valley (2.9 ± 1.7%; Scheffé Post Hoc Test, $P < 0.0001$) and Machine Gun Flats (1.8 ± 1.2%; Scheffé Post Hoc Test, $P < 0.0001$) in April (Fig. 5).

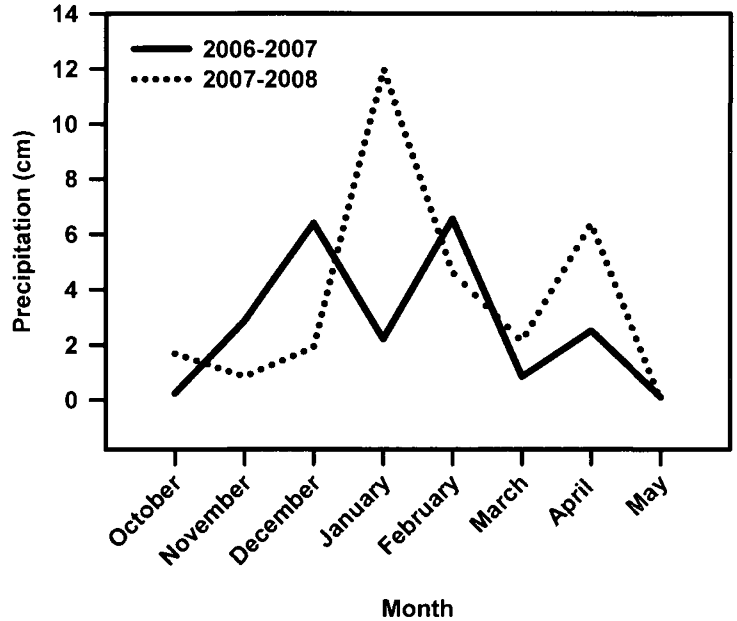

FIG. 3. Average monthly precipitation for Fort Ord, CA between October and May 2006-08 (CDEC 2008).

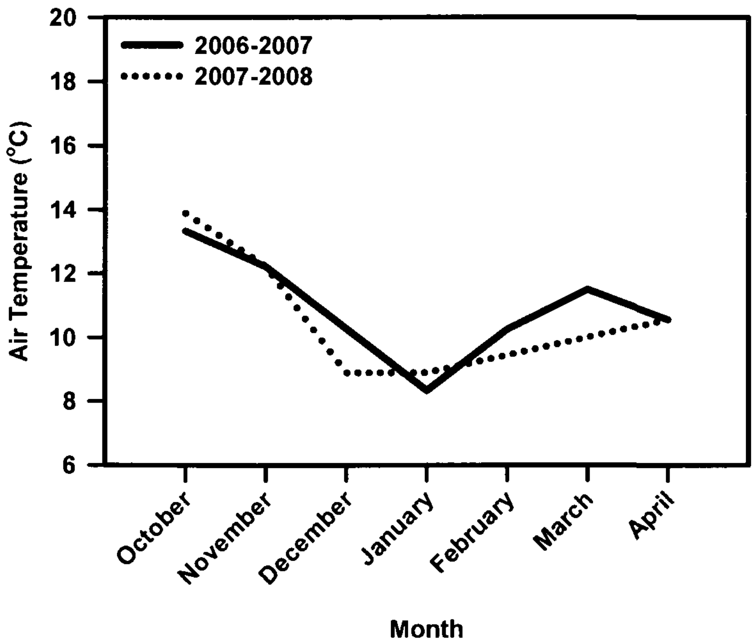

FIG. 4. Average monthly air temperature for Fort Ord, CA between October and May 2006-08 (CDEC 2008).

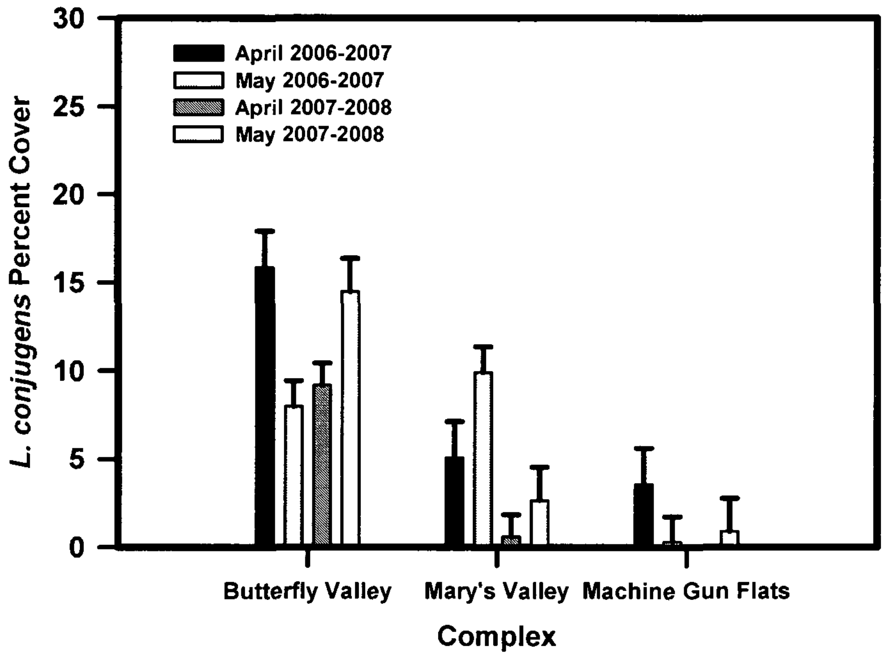

FIG. 5. Average *L. conjugens* percent cover at Fort Ord, CA during two spring seasons. Means $\pm$ SE are shown.

Similar results were observed in May where *L. conjugens* percent cover at Butterfly Valley (12.0 ± 1.7%) was significantly higher than at Mary's Valley (6.3 ± 1.2%; Scheffé Post Hoc Test, P = 0.002) and Machine Gun Flats (0.6 ± 1.1%; Scheffé Post Hoc Test, P < 0.0001). Average *L. conjugens* percent cover in April 2007 across the three complexes was significantly higher than in 2008 (ANCOVA, $F_{1, 174} = 8.16$, P = 0.005), but differences between May 2007 and 2008 were not observed ($F_{1, 174} = 0.09$, P = 0.77).

Significant ecological relationships between *L. conjugens* percent cover and numerous abiotic factors were detected. *Lasthenia conjugens* percent cover was positively related to inundation (Fig. 6; linear regression of the transformed data, r^2 = 0.24, N = 46, P = 0.001), water temperature (Fig. 7; r^2 = 0.17, N = 37, P = 0.011), water pH (Fig. 8; r^2 = 0.15, N = 37, P = 0.019), and water holding capacity (Fig. 9; linear regression of the transformed data, r^2 = 0.14, N = 31, P = 0.042). In addition, *L. conjugens* percent cover in April (r^2 = 0.04, N = 228, P = 0.001) and May (r^2 = 0.03, N = 228, P = 0.005) was found to be weakly related to native species richness.

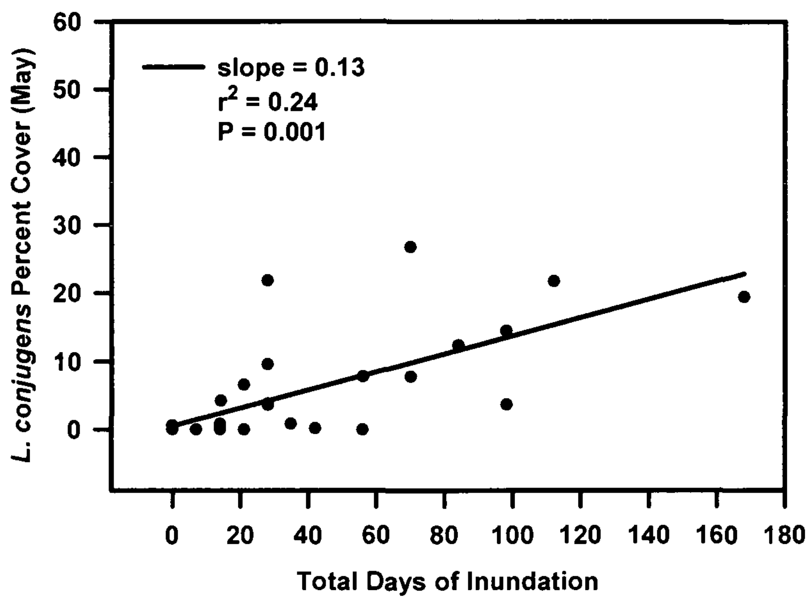

FIG. 6. Relationship of *L. conjugens* percent cover in May and length of inundation at Fort Ord, CA as shown by the linear regression line, Log (y) = 0.51 + 0.13(x).

No significant differences were observed in *L. conjugens* percent cover within the two distinct pool zones (*t*-test, *t* = -0.12, d.f. = 115, P = 0.91). Average *L. conjugens* cover in the pool margins was 3.2 ± 0.65% and 2.4 ± 0.44% in the centers. At Butterfly

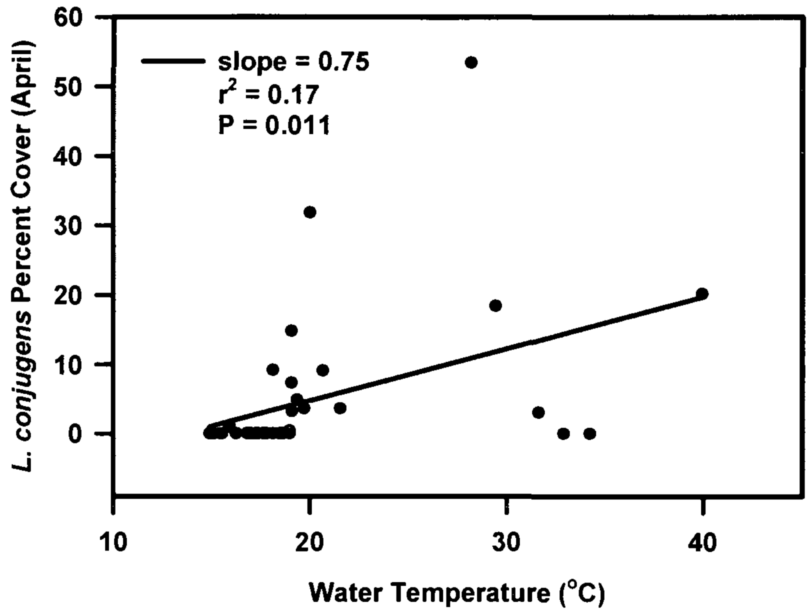

FIG. 7. Relationship of *L. conjugens* percent cover in April and water temperature at Fort Ord, CA as shown by the linear regression line, y = -10.2 + 0.75(x).

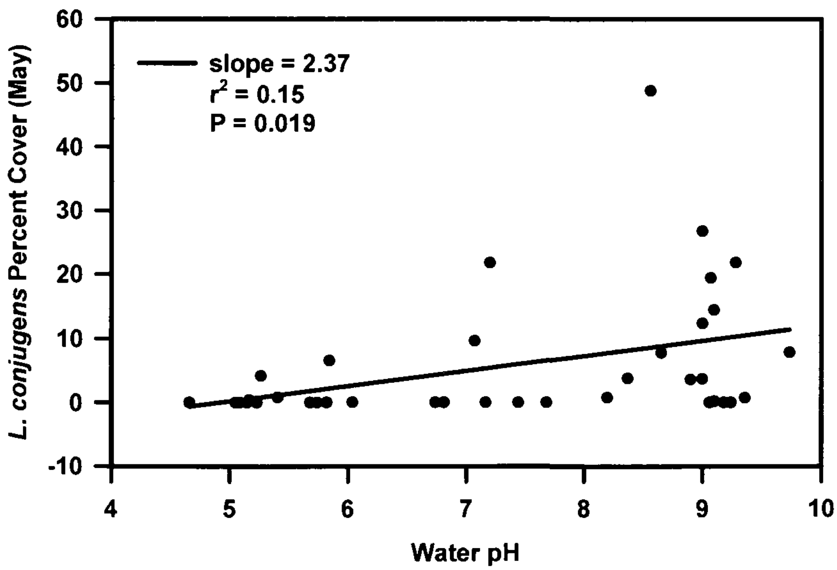

FIG. 8. Relationship of *L. conjugens* percent cover in May and water pH at Fort Ord, CA as shown by the linear regression line, y = -11.67 + 2.37(x).

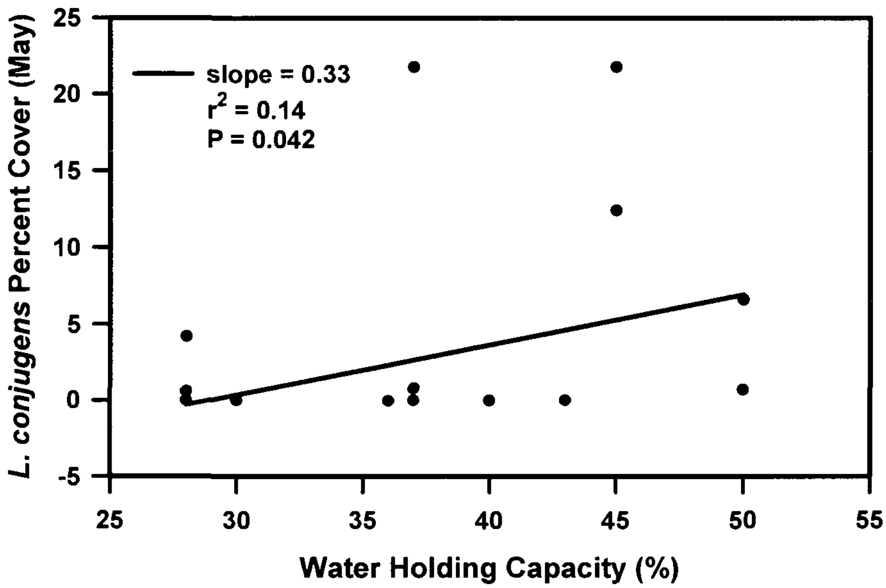

FIG. 9. Relationship of *L. conjugens* percent cover in May and water holding capacity at Fort Ord, CA as shown by the linear regression line, Sin (y) = -9.49 + 0.33(x).

Valley, average cover of *L. conjugens* was 3.9 ± 0.90% in the margins and 3.8 ± 0.65% in the centers. Mary's Valley had lower average cover totaling 2.3 ± 0.39% in the pool margins and 0.7 ± 0.14% in the centers.

Inundation

Given that *L. conjugens* percent cover was positively correlated with inundation, comparisons among complexes with and without *L. conjugens* were conducted to determine if there was a difference. Across the three *L. conjugens* complexes, pools with the rare species did not differ in total days of inundation to pools without it (nested ANOVA, $F_{11, 18} = 0.12$, P = 0.99). Differences across the two sampling years for complexes with *L. conjugens* were not significant (ANCOVA, $F_{1, 32} = 0.19$, P = 0.67). In addition, complexes with *L. conjugens* did not inundate significantly longer than complexes without the rare species (t-test, $t = 0.933$, d.f. = 44, P = 0.36).

Aquatic Environment

Given that *L. conjugens* percent cover was positively related to water temperature and water pH, comparisons among complexes with and without *L. conjugens* were conducted to determine if there were differences. Across the three *L. conjugens* complexes, pools with and without the rare species differed significantly in water temperature (nested ANOVA, $F_{13, 201} = 3.17$, P < 0.0001) and water pH ($F_{13, 201} = 2.55$, P = 0.004) measured at maximum ponding.

Differences were also detected in water temperature (Fig. 10; t-test, $t = -3.15$, d.f. = 168, P = 0.002) and water pH (Fig. 11; $t = -5.09$, d.f. = 168, P < 0.0001) in pools with *L. conjugens* as compared to pools without it among the seven complexes. Pools with the rare endemic were significantly warmer with an average water temperature of 18.1 ± 0.70 °C as compared to pools without it which averaged 13.9 ± 0.86 °C. Pools with the endangered species had significantly higher water pH levels with an average of 7.1 ± 0.25 as compared to pools without it which averaged 4.6 ± 0.28.

Between the two years at the three *L. conjugens* complexes, significant differences in water temperature (ANCOVA, $F_{1, 184} = 7.33$, P = 0.007) and water pH ($F_{1, 184} = 10.17$, P = 0.002) were detected at maximum ponding. With respect to repeated measurements taken throughout the inundation period from December 2007 to March 2008, *L. conjugens* complexes did not contrast significantly from complexes without the endemic in weekly maximum water temperature (RMANOVA, $F_{7, 70} = 0.67$, P = 0.43) and water pH ($F_{7, 70} = 1.98$, P = 0.07).

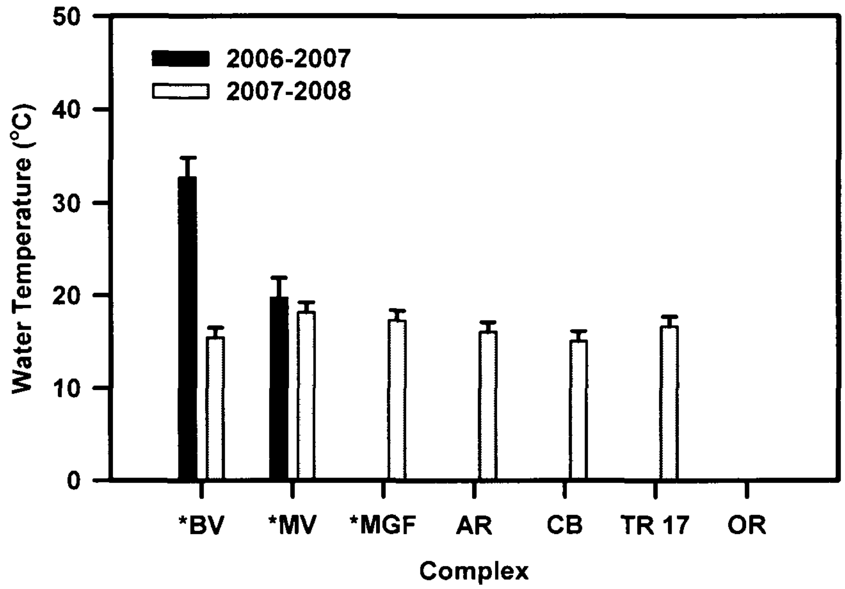

FIG. 10. Average water temperature within the seven complexes at Fort Ord, CA during two spring seasons. Means $\pm$ SE are shown with * denoting complexes with *L. conjugens.* BV = Butterfly Valley; MV = Mary's Valley; MGF = Machine Gun Flats; AR = Addington Road; CB = Crescent Bluffs; TR 17 = Trail 17; OR = Oak Ridge.

Pool Area

Pool area did not correlate to *L. conjugens* percent cover in April (Pearson's correlation, $r = 0.01$, P = 0.98) or May ($r = 0.06$, P = 0.24), nor did it differ between pools with or without *L. conjugens* among the three complexes that harbor the rare species (MANOVA, $F_{1, 44} = 0.25$, P = 0.62). The mean pool area in *L. conjugens* pools over the two wet seasons was 132.9 m^2 whereas pools without it averaged 128.1 m^2.

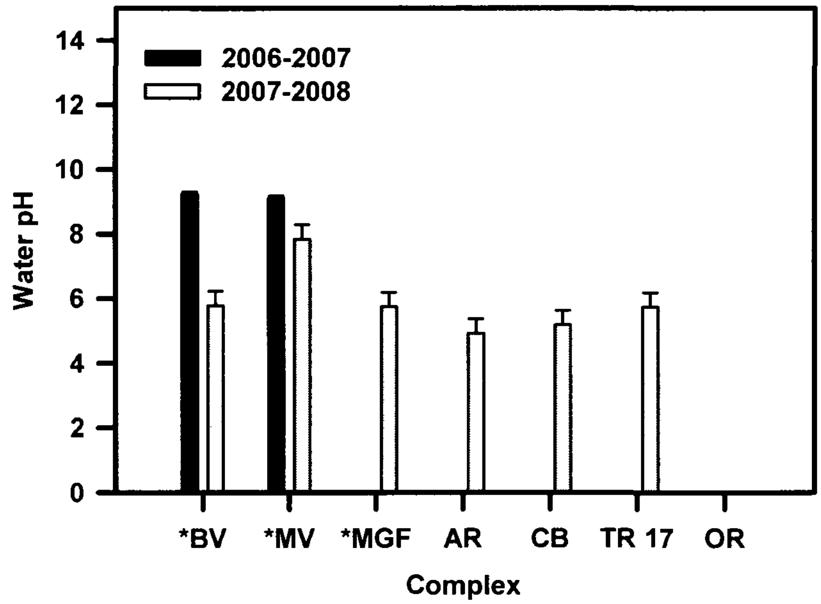

FIG. 11. Average water pH within the seven complexes at Fort Ord, CA during two spring seasons. Means ± SE are shown with * denoting complexes with *L. conjugens*.

Soil Conditions

None of the soil characteristics measured during the sampling period correlated with *L. conjugens* percent cover except for water holding capacity (linear regression of transformed data, $r^2 = 0.14$, N = 31, P = 0.042), nor did they differ between pools with or without *L. conjugens* among the three complexes that harbored the endangered species. Soil characteristics analyzed include ammonium (3.1 ± 0.3 ppm; MANOVA, $F_{1,10} = 0.12$, P = 0.74), nitrate content (0.3 ± 0.1 ppm; $F_{1,10} = 3.62$, P = 0.09), soil moisture (9.2 ± 1.6%; $F_{1,10} = 1.68$, P = 0.22), water holding capacity (35.7 ± 1.2%; $F_{1,10} = 2.69$, P = 0.13), soil pH in $CaCl_2$ (4.9 ± 0.1 pH; $F_{1,10} = 0.28$, P = 0.62), soil pH in deionized water (5.9 ± 0.1 pH; $F_{1,10} = 0.27$, P = 0.61), soil electrical conductivity (180.6 ± 0.2 mS/cm; $F_{1,10} = 0.89$, P = 0.37), and salinity (0.9 ± 0.1%; $F_{1,10} = 0.87$, P = 0.36).

Soil texture between the pools across each complex did not differ significantly: percent sand (39.9 ± 0.3%; MANOVA, $F_{1, 10} = 0.01$, P = 0.92), silt (54.2 ± 0.4%; $F_{1, 10} = 2.36$, P = 0.16), and clay (5.8 ± 0.6%; $F_{1, 10} = 0.06$, P = 0.81). Existing soils mapped by USDA (1961) were verified for four of the seven complexes. The Munsell colors and soil textures at Butterfly Valley, Mary's Valley, Addington Road, and Crescent Bluffs matched the soil series descriptions mapped as Antioch very fine sandy loam, Arnold-Santa Ynez complex, Oceano loamy sand, and Antioch fine sandy loam, respectively. However, field findings for Machine Gun Flats, Trail 17, and Oak Ridge did not match the soil description of Antioch very fine sandy loam as mapped by the USDA (1961). These depressions consisted of silt loam and colors similar to the Arnold-Santa Ynez Complex, with the exception of Oak Ridge. Oak Ridge was the only area dominated by 100% sand and, therefore, was characterized as dissected xerorthents. During the field analysis, the depth to hardpan was reached at Butterfly Valley, Machine Gun Flats, and Trail 17 complexes with depths of 12.7 cm, 35.6 cm, and 38.1 cm, respectively.

Plant Diversity

Given that *L. conjugens* percent cover was positively related to native species richness, comparisons among complexes with and without *L. conjugens* were conducted. Among the three *L. conjugens* complexes, pools with and without the rare species differed significantly in native species richness in April (nested ANOVA, $F_{12, 199} = 2.93$, P = 0.001), but not in May ($F_{12, 199} = 1.63$, P = 0.06).

Native species richness in April differed significantly between pools with the rare endemic as compared to pools without it across all seven complexes (Fig. 12; *t*-test, t =

-5.37, d.f. = 166, $P < 0.0001$). Differences were also detected among the *L. conjugens* complexes as compared to the four alternate complexes with respect to native species richness in May (Fig. 12; *t*-test, $t = -2.72$, d.f. = 226, $P = 0.007$). The average native species richness in *L. conjugens* pools in April was 5 ± 0.2 species whereas in the alternate complexes the average was 4 ± 0.3 species per pool. The average native species richness in *L. conjugens* pools in May was 4 ± 0.1 species whereas pools without the rare endemic averaged 3 ± 0.2 species.

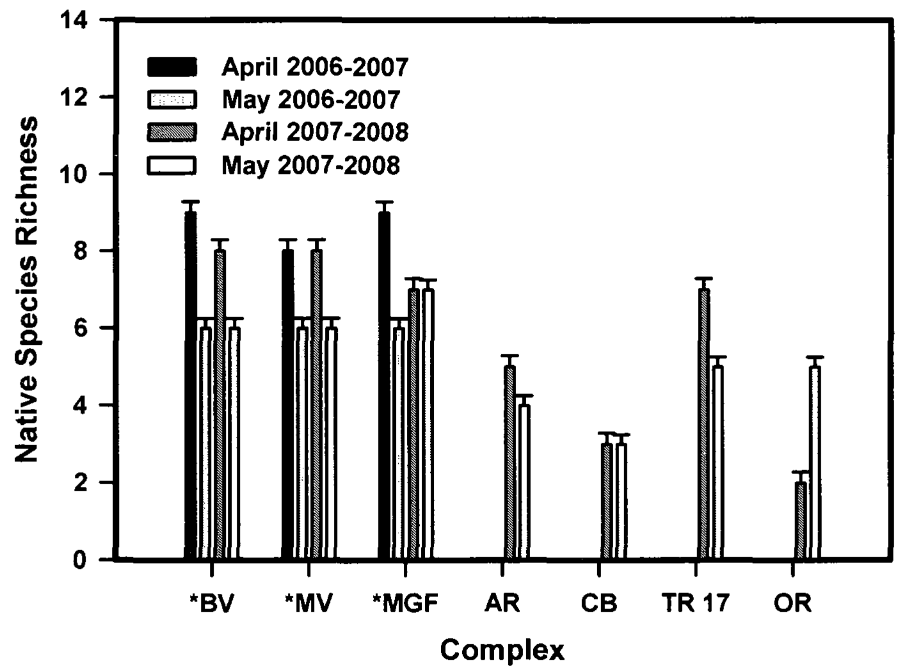

FIG. 12. Average native species richness within the seven complexes at Fort Ord, CA during two spring seasons. Means $\pm$ SE are shown with * denoting complexes with *L. conjugens.*

Pig Disturbance

Pig disturbance was not related to *L. conjugens* percent cover in April (linear regression, $r^2 = 0.01$, N = 143, $P = 0.18$) or May ($r^2 = 0.001$, N = 143, $P = 0.85$) nor was it related to bare ground cover in April (linear regression of transformed data, $r^2 = 0.01$, N = 143, P = 0.20) or May ($r^2 = 0.004$, N = 143, P = 0.42). However, it was weakly related to native species richness in April ($r^2 = 0.11$, N = 143, P < 0.0001). As pig disturbance percent cover increased, native species richness increased. Given that pig disturbance percent cover was positively related to native species richness, comparisons among complexes with and without *L. conjugens* were conducted. Percent cover of pig disturbances within *L. conjugens* pools did not differ significantly from pools without the endangered species (MANOVA, $F_{1, 141} = 0.39$, P = 0.54).

However, significant differences were detected for several abiotic and biotic factors when analyses were conducted with respect to pig presence or absence. Water temperature (nested ANOVA, $F_{20, 194} = 28.65$, P < 0.0001), electrical conductivity ($F_{20, 194} = 4.74$, P < 0.0001), *L. conjugens* percent cover in April (nested ANOVA, $F_{18, 244} = 11.66$, P < 0.0001) and May ($F_{18, 244} = 9.09$, P < 0.0001), native cover in April (nested ANOVA, $F_{18, 192} = 3.24$, P < 0.0001), and native species richness in April ($F_{18, 192} = 5.42$, P < 0.0001) were significantly higher in pools with pig disturbance (Table 1).

Lasthenia conjugens Floral and Vegetative Traits

Significant differences in floral and vegetative traits among *L. conjugens* complexes were not observed for any of the traits measured: plant height (71.9 ± 0.2 mm; nested ANOVA, $F_{3, 35} = 0.15$, P = 0.93), inflorescence diameter (10.5 ± 0.6 mm; $F_{3, 35} = 0.33$, P = 0.89), disk diameter (4.5 ± 0.3 mm; $F_{3, 35} = 1.29$, P = 0.29), ray length (3.4 ± 0.2 mm; $F_{3, 35} = 0.75$, P = 0.53), and number of ray flowers (8 ± 0.3; $F_{3, 35} = 0.78$, P = 0.55). Significant differences across the two sampling years were observed for disk diameter

(ANCOVA, $F_{1, 40} = 22.85$, $P < 0.0001$) and ray length ($F_{1, 40} = 5.64$, $P = 0.022$), where traits were larger in 2008.

Table 1. Mean (± SE) comparisons of biotic factors in pools with and without pig disturbance.

Biotic Factors	Pools with pig disturbance Mean (±SE)	Pools w/o pig disturbance Mean (±SE)
L. conjugens % Cover –April	7.04 (1.49)	1.39 (0.38)
L. conjugens % Cover – May	5.99 (1.32)	2.49 (0.70)
Native % Cover – April	54.02 (3.13)	61.03 (3.25)
Non-Native % Cover – April	10.90 (1.38)	14.85 (1.75)
Bare ground % Cover – May	17.42 (2.01)	9.5 (1.60)
Native Species Richness – April (# of species)	5 (0.18)	4 (0.18)
Plant Height (mm)	78.84 (0.90)	43.73 (0.80)
Inflorescence Diameter (mm)	11.81 (0.52)	5.07 (1.08)
Disk Diameter (mm)	5.07 (0.25)	2.29 (0.48)
Ray Length (mm)	3.76 (0.14)	1.73 (0.32)

Lasthenia conjugens vegetative and floral traits were larger in pools with pig presence (Table 1). These traits include plant height (MANOVA, $F_{1, 44} = 8.12$, $P = 0.007$), inflorescence diameter ($F_{1, 44} = 6.01$, $P = 0.018$), disk diameter ($F_{1, 44} = 23.83$, $P < 0.0001$), and ray length ($F_{1, 44} = 39.57$, $P < 0.0001$).

DISCUSSION

These field studies illustrate that the success of *L. conjugens* at Fort Ord is likely determined by a combination of abiotic and biotic parameters, including seasonal inundation, water chemistry, soil-nutrient properties, and disturbance history. *Lasthenia conjugens* was most abundant in pools at Butterfly Valley, which, of the three complexes, averaged well above the mean for most of the related factors. The smallest population at Machine Gun Flats had significantly shorter periods of inundation, lower water pH, and lower native species richness as compared to Butterfly and Mary's Valleys. Therefore, it appears that this rare endemic has an ecological tolerance for varying conditions in both the abiotic and biotic environment found at the southern edge of its distribution. However, the data suggest that *L. conjugens* thrives in pools with longer inundation regimes, deeper and warmer waters, higher native cover, and greater native species richness, as seen in Butterfly and Mary's Valleys.

The four alternate complexes that lack this rare endemic appear to fall out of the mean ecological range for several of the factors related to *L. conjugens* abundance, including water temperature, water pH, and native species richness. These abiotic and biotic parameters were significantly lower on average at the four alternate complexes when compared to *L. conjugens* complexes.

Consequently, when the maximum and minimum values for all factors measured were compared in pools with and without the rare endemic, Addington Road, Crescent Bluffs, and Trail 17 pools showed a trend toward the minimum ranges observed in *L. conjugens* pools for a majority of the related factors. Inundation regime, water temperature, and water pH at the three alternate complexes were much like the conditions found at *L. conjugens* pools within Machine Gun Flats. In addition, these pools were found to be within the minimum ecological range of *L. conjugens* pools with respect to soil conditions, native and non-native percent cover, and native and non-native species richness. Therefore, these complexes would likely support *L. conjugens*, but the total percent cover would be significantly lower as seen at Machine Gun Flats. Thus, it appears that the four alternate complexes would be unsuitable for successful introduction efforts of *L. conjugens* at the present time. In the sections that follow, the essential roles of each abiotic and biotic factor investigated in this study and their implications for species recovery regarding *L. conjugens* at Fort Ord are further explored.

Abiotic Factors

Seasonal inundation is important in controlling community structure of vernal pools (Holland and Jain 1984). The presence of water in this microhabitat produces anaerobic conditions that decrease decomposition rates and discontinue a variety of chemical and biological interactions typical of terrestrial conditions, creating a harsh environment for plant growth (Gerhardt and Collinge 2003). For instance, seasonal ponding reduces the readily available oxygen and nutrients in the soil, decreases light and carbon dioxide levels, as well as halts the symbiotic relationships between plants and nitrogen-fixing microbes (Crawford 1992). This depleted environment excludes a majority of non-native and upland species in surrounding habitats. As a result, vernal pool specialists such as *L. conjugens* have evolved morphological and physiological traits that are well adapted to these wet conditions and dependent on them for germination cues, seedling resource competition, and reproductive success (Baskin 1994).

Some vernal pool species, such as *E. macrostachya,* require long-inundated, deep pools while others such as *Layia fremontii* A. Gray (Fremont's tidy tips; Asteraceae) can only tolerate shallow pools with short ponding regimes. In complexes with both types of specialists, the center of a given pool will have water present for longer periods, as this is typically the deepest part of the depression, and will be dominated by long-inundated pool species with the edges dominated by the short-inundated specialists. Thus, many vernal pool ecosystems exhibit specific pool zones dominated by a select number of species as one moves from the center to the edges of a given pool (Holland and Jain 1984). This species-specific pool zonation, seen during the blooming season as concentric rings of different floral colors, is directly related to periods of inundation, water depth, and soil water holding capacity (Barbour et al. 2003).

Lasthenia conjugens has been repeatedly reported from long-inundated pools but is also known from short-inundated pools within its range indicating its tolerance for variable inundation regimes (Ornduff 1966; USFWS 2005a). The depressions at Butterfly Valley, Mary's Valley, and Trail 17 can be characterized as long-inundated, deep pools in contrast to the other four complexes, which were delimited by periods of short inundation and shallow waters. Although inundation did not differ significantly among the seven complexes, prolonged periods of ponding at Butterfly and Mary's Valley correlated to higher *L. conjugens* percent cover. Therefore, the data suggest that the alternate complexes are marginal with respect to inundation requirements necessary for successful introduction efforts of this vernal pool endemic.

The chemical integrity of the aquatic environment plays a critical role in germination and seedling success of rare endemics such as *L. conjugens* (Brady and Weil 2008). Temporary pooling warms the soil temperatures in the beginning of the growing season, which for most wetland species initiates germination. Sufficient levels of dissolved oxygen, dissolved salts, and neutral water pH are vital to physiological processes, such as photosynthesis and respiration, during the seedling stage as these factors highly correlate with soil pH and cation exchange capacity (Brady and Weil 2008). Pools with higher water pH and electrical conductivity were found to have higher soil pH and ion availability, which directly affect the nutrient values present during the growing season. During the 2007-08 wet season, the aquatic environment at the four alternate complexes did not achieve mean values for any of the aqueous factors measured in *L. conjugens* pools. Although the data were collected for only one sampling year, it suggests that Addington Road, Crescent Bluffs, Trail 17, and Oak Ridge are unsuitable with respect to water chemistry requirements for *L. conjugens*.

Soil conditions such as ion availability and pH also play a determining role in the presence and dominance of vernal pool species (Holland and Dain 1990). During the wet season, vernal pools are characterized by oxygen-depleted soils that have lower available cations, as they become the main electron acceptors for several stages driving plant respiration. Anoxia also increases iron content, which in turn decreases soil pH (Brady and Weil 2008). Soil pH is vital to plants in that it influences the solubility of dissolved ions within the soil that plants require for photosynthesis (Rajakaruna and Boyd 2008). Lower levels of pH limit the solubility of several important compounds necessary for water uptake and cation exchange, thus increasing resource competition among native populations. Vernal pool specialists have evolved ways to cope with oxygen deficits and nutrient restrictions, including prominent air spaces in the root cortex and metabolic regulation (Marschner 1995).

The soil and nutrient factors examined in this study suggest that *L. conjugens* pools had a slightly acidic environment with moderate nutrient levels, where alternate pools were lower in all values with the exception of soil moisture and pH. Although the soil factors quantified in this study, including nitrogen availability, soil pH, salinity, and water holding capacity, did not differ significantly between pools with and without *L. conjugens*, it is difficult to conclude whether edaphic parameters would be suitable for introduction efforts because the soil environment was minimally sampled due to monetary constraints and agency permit issues. The one sample collected in the middle of each pool (which excluded *L. conjugens* to avoid impacts to the sensitive species) during the early blooming period was not a thorough method of surveying the edaphic environment throughout the pool basins. Soil nutrients and pH may differ from the center of a pool to its edge during critical phases, including germination, flowering, and seed set (Marschner 1995; Rajakaruna and Bohm 1999). Therefore, future soil collections from the perimeter to the center of a given pool during these three phases are proposed this spring. The conclusions regarding the soil environment will be published elsewhere after field and laboratory results are completed.

Biotic Factors

Native species diversity is an important biotic factor, as suggested by the positive relationship between *L. conjugens* abundance and native species richness during the early blooming period. In addition, *L. conjugens* abundance had a positive relationship with inundation, water temperature, and water pH, suggesting that pools with increased values of these parameters would also contribute to the native structure and composition of *L. conjugens* pools at Fort Ord. The data also suggest that the biotic interactions seen in *L. conjugens* pools at Butterfly and Mary's Valley support the biotic resistance hypothesis that increased native cover and diversity help prevent exotic establishment (Gerhardt and Collinge 2003). Pools at Machine Gun Flats resulted in higher cover and number of non-natives, suggesting that other exclusionary factors such as inundation, water chemistry, and anaerobic soil conditions are not prevalent enough to resist exotic invasions. Non-natives including *Plantago coronopus* L. (buckhorn plantain; Plantaginaceae), *Geranium dissectum* L. (cutleaf geranium; Geraniaceae), and *Erodium botrys* (Cav.) Betrol (longbeak filaree; Geraniaceae), which can tolerate mesic conditions, were commonly seen in high abundance at Machine Gun Flats and the four alternate complexes. Non-native cover had a negative relationship with inundation, signifying the importance of the exclusionary factor brought with the presence of water in this sensitive habitat. Characterized by shorter inundation regimes and higher non-native diversity, Machine Gun Flats and the four alternate complexes are not equipped with the abiotic and biotic conditions that are essential for exotic resistance. Therefore, these complexes appear to have marginal to unsuitable habitat with respect to *L. conjugens* restoration.

Pig disturbance appears to be another key factor that contributes specifically to soil nutrients and native cover in the vernal pools at Fort Ord. Pools with high pig activity resulted in higher ammonium levels, bare ground, and *L. conjugens* percent cover as compared to pools with no pig disturbance. In addition, percent cover of pig disturbance related positively with native species richness. This relationship indicates that pigs may be more attracted to the pools with greater native diversity or that pig disturbance may increase native species richness. Future investigations will be conducted to test whether or not pig disturbance enhances native species diversity.

With respect to *L. conjugens* percent cover and traits, pools with high intensity of pig disturbance, mainly at Butterfly Valley, had the highest cover and the largest vegetative and floral traits. Thus, pools with pig activity may positively influence the overall seed production and population growth. In addition, increased bare ground and ammonium content at Butterfly Valley significantly exceeded all other complexes, suggesting that pig activity (including the presence of pig scat) may be the culprit for increased abundance and overall plant traits of *L. conjugens*. To further understand the relationship between pig activity and *L. conjugens* reproductive fitness, future monitoring of pig activity and *L. conjugens* cover and seed production at Fort Ord is planned for the next two years.

Conclusions

In light of these results, *L. conjugens* appear to thrive in pool basins that are characterized by long inundation regimes with warm waters and neutral water pH during the wet season. General edaphic conditions optimal for this rare endemic include high water holding capacity, moderate levels of soil moisture and electrical conductivity, and low soil pH during the growing season. Pools dominated by native vernal pool specialists with little non-native cover also appear to be a necessary requirement for *L. conjugens* success. Thus, the four alternate complexes and the pools without *L. conjugens* at Butterfly Valley, Mary's Valley, and Machine Gun Flats do not appear to be suitable for introduction efforts for this rare species.

Once the edaphic conditions are further explored, new sites can be field verified for seasonal inundation, water chemistry, soil and nutrient factors, and disturbance history for planned introduction strategies. In addition, to test some of the main abiotic requirements of *L. conjugens*, greenhouse studies on varying inundation regimes and soil pH are recommended for this population. Due to the variation of pool hydrology and soil pH at Fort Ord, it is crucial to understand the thresholds for successful *L. conjugens* growth and reproduction with respect to important abiotic parameters.

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