

Patterns of Vernal Pool Biodiversity at Beale Air Force Base

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ABSTRACT. The effects of substrate geomorphic surface and physical vernal pool dimensions on plant species richness and composition, and large branchiopod occurrences were investigated for 814 vernal pools at Beale Air Force Base, Yuba County, California. Vernal pools mostly occurred on four geomorphic surfaces: the Mehrten, Laguna, Riverbank, and Modesto Formations. Plant species richness was positively correlated to vernal pool depth and surface area, but did not vary among geomorphic surfaces. Plant species composition differed significantly among geomorphic surfaces, although much overlap in species composition among surfaces was apparent. Depth and surface area strongly affected vernal pool plant species composition. Two rare plant species were found: *Downingia pusilla* and *Legenere limosa*. Active *Branchinecta lynchi* (Vernal Pool Fairy Shrimp) were found in 16.1% of pools and eggs in 15.8%. Occurrence of eggs was a poor predictor of occurrence of active specimens. *Branchinecta lynchi* egg or active specimen occurrences did not differ significantly among geomorphic surfaces. The frequency of occurrence of active *Lepidurus packardii* (Vernal Pool Tadpole Shrimp) specimens was 2.8%. Active *L. packardii* were found only in Modesto and Riverbank Formation pools. Active *Linderiella occidentalis* (California Linderiella) were found in 22.7% of vernal pools, but eggs were retrieved from 7 pools (1%) only. *Linderiella occidentalis* occurrence differed significantly among geomorphic surfaces. Frequency of occurrence of active fairy shrimp increased significantly with pool depth. *Branchinecta lynchi* egg occurrence also increased significantly with pool depth. Species differed in their response to pool surface area. The ecological relationships found in this study can help in designing a conservation strategy for biological diversity in the vernal pool landscape at Beale Air Force Base and in other Sacramento Valley areas.

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INTRODUCTION

Vernal pools are characterized by high levels of biological diversity, and have been described as “complex ecological systems” (Holland and Dains, 1990). The diversity of vernal pool plant species has long been appreciated (Holland and Jain, 1977), and more recently the high diversity of crustacean species has been recognized (e.g., King et al., 1996). A major source of complexity is that factors that determine species composition and diversity vary among spacial scales.

State-wide patterns in plant species composition are best explained by climate and source biota that vary with latitude (Holland and Jain, 1981; Holland and Dains, 1990). At a “meso-scale,” the scale defined by the size of a county, soil factors such as those that determine differences among soil mapping units may explain patterns in plant species composition, when site history is factored out (Holland and Dains, 1990). Holland and Dains’ (1990) data suggest that older soils differ from younger soils in species composition, presumably because old soils have a shallower impervious soil layer and therefore a lower soil moisture holding capacity. Jokerst (1990) found that volcanic mudflow pools are not botanically distinct from pools

on other geomorphic surfaces, although soil depth was an important determinant of species composition, together with soil texture, vernal pool topography, surface area and depth. Holland and Dains (1990) found that at the local scale, i.e., within one soil mapping polygon, the depth to the hardpan and hydrologic conditions may determine the distribution of individual species.

Plant species diversity is determined, in part, by vernal pool area and depth (Holland and Jain, 1981; Rosario and Lathrop, 1984; Jokerst, 1990). This could simply be the result of the larger number of niches afforded by a larger or deeper vernal pool (Holland and Jain, 1981; 1984). In addition, Holland and Jain (1984) found that in wet years plant species diversity is higher than in dry years, suggesting that the duration of ponding affects plant species diversity.

The number of crustacean species in vernal pools increases also with vernal pool surface area (Ebert and Balko, 1984). However, Ebert and Balko (1984) caution that not only space, but also other habitat parameters, including temporal habitat availability may play an important role in determining diversity. Recently, King et al. (1996) found also that crustacean species

diversity increases with increasing vernal pool area and depth. They found that crustacean species composition is affected in addition by water chemistry, elevation and biogeographic province.

In this paper, I will explore to what extent geomorphic surface, vernal pool depth and surface area explain patterns of plant species richness and composition and the occurrence of large branchiopod crustaceans in the vernal pools of Beale Air Force Base in the northern Sacramento Valley. The objective of the analysis is to determine whether information on geomorphic surface, pool depth and surface area can help design conservation strategies for vernal pools at Beale Air Force Base. The study is part of an ongoing habitat conservation planning process for vernal pools at Beale Air Force Base conducted by the U.S. Air Force.

METHODS

Study Site

Beale Air Force Base is located in the northeastern portion of the Sacramento Valley, California, approximately 55 km N of Sacramento and 13 km E of Marysville, elevation 24–180 m. The areal extent is approximately 9,500 ha, and approximately 8,000 ha is undeveloped. The undeveloped area consists almost exclusively of grasslands.

Five major geomorphic surfaces can be distinguished at Beale Air Force Base (Table 1). The extent of vernal pools, as mapped from aerial photographs, differs markedly among geomorphic surfaces (Figure 1, Table 1). Grasslands underlain by metavolcanic bedrock have a very low vernal pool cover (0.03%), these pools will not be considered here. The Mehrten Formation is of Miocene volcanic origin and has relatively low cover of vernal pools (0.3%). The Laguna Formation is of alluvial Pliocene origin and has 1.3% cover of vernal pools. The Riverbank Formation is of alluvial early Pleistocene origin and has the highest cover of vernal pools (2.8%). The youngest surface, the Modesto Formation, is late Pleistocene alluvium and has approximately half the vernal pool cover of the Riverbank Formation.

Most of the grassland is grazed by cattle, although some areas, in particular near the runway, have not been grazed for decades.

Sampling

Vernal pools and other seasonal wetlands at Beale Air Force Base were randomly selected by placing 1,000 points with random coordinates on a map of seasonal wetlands of the undeveloped portion of the base. The nearest seasonal wetland to each random point was sampled. Natural vernal pools comprised 814 of these wetlands, 56 were the result of accidental human dis-

TABLE 1. Undeveloped areal extent of geomorphic surfaces and vernal pools at Beale Air Force Base.

Geomorphic Surface	Area (ha)	Vernal pool area (ha)	% vernal pool area
Modesto Formation	1,714	24.0	1.4
Riverbank Formation	2,509	70.4	2.8
Laguna Formation	1,632	21.2	1.3
Mehrten Formation	900	2.8	0.3
Metavolcanic Bedrock	2,880	0.4	0.03
TOTAL	7,921	118.8	1.5

turbances (e.g., ditches and tire ruts) and 130 were seasonal swales and other seasonal wetlands. I will discuss results from natural vernal pools only in this paper.

Invertebrates. From October 11 to November 7, 1995, at the end of the dry season, the randomly selected seasonal wetlands were sampled for eggs of large branchiopod crustaceans, i.e., anostracans and notostracans. A thin layer (< 1 cm deep) of surface sediment was collected with a hand trowel from 10 locations from the bottom portions of each wetland. The 10 locations were chosen to maximize the probability of finding crustacean eggs, and therefore were mostly taken in deeper part of the pool and in suitable micro sites, such as hoof prints. This method leads to a significantly higher probability of finding branchiopod eggs than using random sampling (Jones & Stokes Associates, unpublished data). The ten samples from one pool were combined in one container prior to storage.

Soil samples were sieved and the particle fraction between 150 and 500 μm was examined under a binocular dissecting microscope. Published scanning electron micrographs (Gilchrist, 1978; Mura, 1991) and Jones & Stokes Associates' reference collection were used to identify the collected eggs to species. *Branchinecta* eggs in three samples that could not be identified to species were assumed to be eggs of *B. lynchi*. In some cases empty protein coats (egg casings) of *B. lynchi* eggs were found. For this analysis, these protein coats were assumed to represent the presence of *B. lynchi* in a pool. In total, 987 seasonal wetlands were sampled; 126 contained protein coats, and 40 contained *B. lynchi* eggs. Notostracan eggs (e.g., eggs of *Lepidurus*) were not reliably identified and will not be discussed in this paper.

Each randomly selected vernal pool was sampled three times for active large branchiopods during the wet season, which generally extends from November to April. A 150 μm mesh net with an aperture of 452 cm^2 was pulled for 1 m over the bottom of each vernal pool. Any large branchiopods in the net were identified to species using a 18x magnifying hand lens and released. This sampling method was repeated until three species of large branchiopod were caught or the entire pool was sampled.

FIGURE 1. Geomorphic surfaces at Beale Air Force Base and distribution of vernal pools.

The sampling dates were chosen to follow rain storms during the cold part of winter and during early spring. The three sampling periods were: January 8-January 19, 1996, February 13-March 1, 1996, and March 25-April 4, 1996.

During the invertebrate sampling, the maximum pool depth at the deepest point of the pool was measured (or estimated, when the pool was not at maximum depth) and the area of the maximum ponded area was measured by pacing the average width and length of a pool and then multiplying these two measurements.

Plants. Plant surveys were conducted from March 12, 1996 to May 29, 1996. Vernal pools were sampled when most species in the pool were flowering. Some deep pools were sampled twice, because a portion of the pool was still ponded when they were sampled. All plant species present below the high water mark were recorded.

Total vegetative cover for the pool was estimated and five species with the highest cover were given a relative abundance score according to the following scale: * = <1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, and 5 = 76-100%. The percentages represent relative vegetative cover for the pool. Absolute vegetative cover was also recorded. All cover estimates refer to cover of a projection on a plane parallel to the soil surface. All plants that were present in a pool, but that were not among the top five dominants, or that had a score < 1% were given a relative abundance score of 0.1.

Only those plant species that are considered "Central Valley vernal pool plant species" were considered in the analysis. Central Valley vernal pool species are native plants which are either vernal pool obligates or, at least when found in the Central Valley, more frequently occur in vernal pools than in other habitats. These are species placed on a list by the U.S. Army Corps of Engineers (1994) after extensive review by local botanists. The total number of taxa in all seasonal wetlands was 214, but only 44 species fit the above definition. Limiting the analysis to these 44 species reduced the number of variables in multivariate analysis of species composition, and reduced the potential to violate assumptions of multivariate tests, while maintaining a focus on native wetland resources.

Data Analysis

All statistical tests involving vernal pool depth and area were performed on ln-transformed area and depth, which improved normality of the data and normality of residuals. Vernal pool plant species richness, i.e., the number of vernal pool plants per pool, was also significantly right-skewed (skewness = 0.38). Therefore, species richness data were square-root transformed prior to analysis, which yielded a distribution that was close to normal. The square-root is an appropriate transformation for

counts (Sokal and Rohlf, 1981). However, regressions of species richness on pool depth and area were performed on ln-transformed data, to make the results comparable to previously published regressions of this kind (Holland and Jain, 1981; Jokerst, 1990). Although tests were performed on transformed data, means and standard errors were reported for untransformed data, to facilitate interpretation.

Plant species composition was analyzed using canonical discriminant analysis, also known as canonical variate analysis, and canonical correlation analysis. This multivariate technique is suitable when the number of samples is larger than the number of variables (i.e., species). The results of hypothesis tests should be interpreted with caution, because this technique assumes that the data are multivariate normally distributed. An accessible discussion of these techniques is given in ter Braak (1987).

Presence or absence of crustacean species as a function of vernal pool size or depth was analyzed using multiple logistic regression on ln-transformed data. Logistic regression is a technique that utilizes continuous independent variables and binary dependent variables. An accessible discussion of this technique is provided in ter Braak and Looman (1987) and Fienberg (1980).

All data analysis was performed with SAS Version 6 (SAS Institute, 1990a; 1990b).

RESULTS

Vernal Pool Dimensions

Mean vernal pool area differed significantly among geomorphic surfaces ($F = 12.9$; $df = 3, 811$; $P < 0.0001$). A multiple range test indicated that Modesto and Riverbank Formation pools had a significantly greater mean area than Laguna and Mehrten Formation pools ($P < 0.05$), but that within these two groups the mean pool area did not differ (Figure 2).

Mean depth also differed significantly among geomorphic surfaces ($F = 18.2$; $df = 3, 810$; $P < 0.0001$). Modesto Formation pools were deeper than Riverbank and Laguna Formation pools. Mehrten Formation pools were shallower than Riverbank and Laguna Formation pools ($P < 0.05$; Figure 3).

Plant Species Richness

The mean number of vernal pool plant species per pool did not differ significantly among geomorphic surfaces ($F = 2.42$; $df = 3, 782$; $P = 0.06$). The least-squares means varied from 10.0 for the Modesto Formation to 11.0 plants per pool for the Riverbank Formation. When the natural log of pool depth was entered as a covariate the difference among geomorphic surfaces became

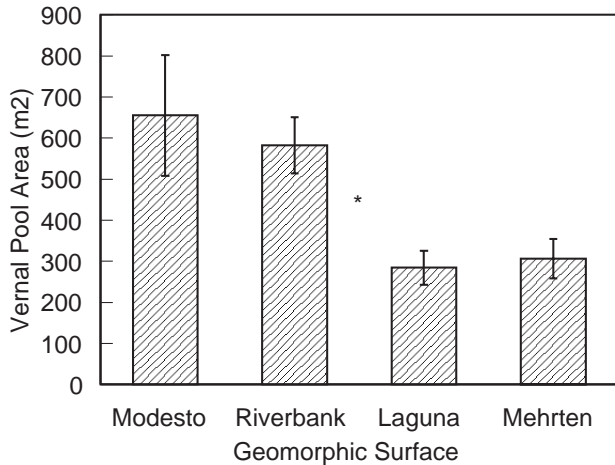


FIGURE 2. Mean vernal pool area on four geomorphic surfaces (formations). Error bars represent ± 1 standard error. * indicates that adjacent means are significantly different by the Student-Newman-Keuls multiple range test ($P < 0.05$).

even smaller ($F = 1.99$; $df = 3, 782$; $P = 0.11$), but the effect of the covariate was highly significant ($F = 23.9$; $df = 1, 782$; $P < 0.0001$), indicating that the difference among formations was largely attributable to differences in pool dimensions.

The regressions of the natural log of vernal pool plant species per pool on the natural logs of pool area and depth were both statistically significant, although these relationships explained only a small portion of the variation in vernal pool species richness ($r^2 = 5.7\%$ and 6.3% , for area and depth, respectively). The fit of a multiple regression model was somewhat better (Table 2).

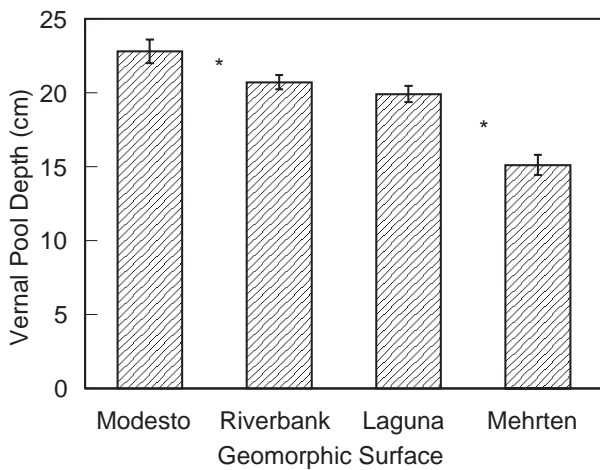


FIGURE 3. Mean vernal pool depth on four geomorphic surfaces (formations). Error bars represent ± 1 standard error. * indicates that adjacent means are significantly different by the Student-Newman-Keuls multiple range test ($P < 0.05$).

TABLE 2. Regressions of vernal pool plant species richness (S) on pool area and depth.

Equation	r^2 (in %)	P
1. $\ln(S) = 0.081 \ln(\text{area}) + 1.85$	5.7	0.0001
2. $\ln(S) = 0.262 \ln(\text{depth}) + 1.51$	6.3	0.0001
3. $\ln(S) = 0.059 \ln(\text{area}) + 0.201 \ln(\text{depth}) + 1.38$	9.0	0.0001

Plant Species Composition

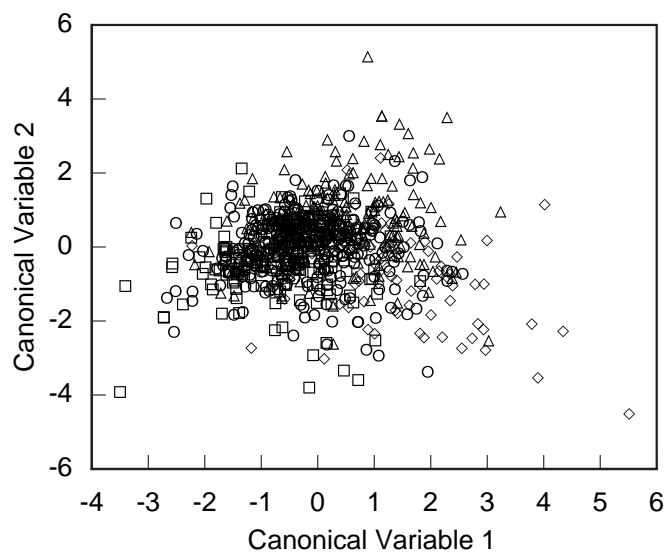
A canonical discriminant analysis of vernal pool species abundance scores indicated that species composition differed significantly among geomorphic surfaces (Wilk's Lambda = 0.84; $F = 1.9$; $df = 88, 1836$; $P < 0.0001$). The multivariate distance between means for geomorphic surfaces based on species abundance scores tended to increase with increasing age difference between geomorphic surfaces (Table 3).

Plots of canonical variable scores for individual vernal pools showed that although there was considerable overlap among geomorphic surfaces, differences among surfaces were also apparent (Figures 4 and 5). For example, Figure 4 shows that Mehrten and Laguna Formation pools tended to score relatively high on the first canonical axis, while Riverbank and Modesto Formation pools tended to score relatively low on this axis. Figures 4 and 5 show that Laguna Formation pools tended to score relatively high on the second canonical axis.

Two sets of variables, the first representing vernal pool species abundances and the second representing a combination of pool depth and area were entered in a canonical correlation analysis. The first canonical correlation between these two sets of variables was 0.59 ($F = 5.09$; $df = 88, 1480$; $P < 0.0001$), and the second canonical correlation was 0.31 ($F = 1.84$, $df = 43, 741$; $P < 0.001$), showing that vernal pool area and depth strongly affected plant species composition. Figure 6 shows the relationship between the first two canonical variables. Both pool area and pool depth were positively correlated with the first

TABLE 3. Squared Mahalanobis distances between multivariate means for geomorphic surfaces based on vernal pool plant species abundance scores (above diagonal), with univariate F-statistics with $df = 44, 740$ (below diagonal).

	Modesto	Riverbank	Laguna	Mehrten
Modesto	0	0.96	2.01	4.17
Riverbank	2.13	0	0.89	3.00
Laguna	3.91	2.55	0	2.90
Mehrten	4.83	4.31	3.82	0



□ Modesto ○ Riverbank △ Laguna ◇ Mehrten

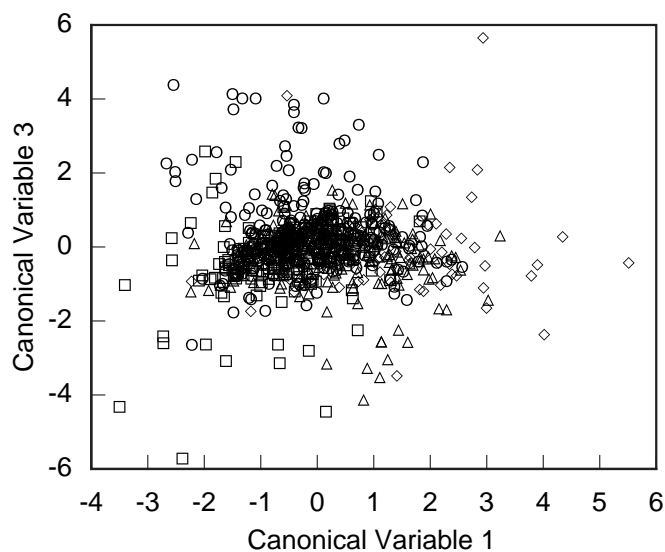
FIGURE 4. Ordination of vernal pools by the first and second canonical variables of a canonical discriminant analysis of vernal pool plant species abundance scores for four geomorphic surfaces.

canonical variable for pool dimension ($r = 0.67$ and $r = 0.92$, respectively). Plant species with a high positive correlation with the first canonical variable are expected to dominate deeper or larger pools. These species were *Downingia bicornuta* ($r = 0.56$), *Eryngium castrense* ($r = 0.41$), *Lasthenia glaberrima* ($r = 0.39$) and *Ranunculus bonariensis* var. *trisepalus* ($r = 0.37$). Species with the lowest negative correlations with the first canonical variable for species composition are expected to dominate smaller or shallower pools. These species were *Deschampsia danthonioides* ($r = -0.49$), *Pogogyne zizyphoroides* ($r = -0.29$) and *Lasthenia fremontii* ($r = -0.28$).

Partial canonical correlations, multivariate extensions of ordinary partial correlations, were calculated to further investigate the response of species to pool depth and area, separately. Figure 7 shows that most species that dominated large pools also dominated deep pools, and species that dominated shallow pools, also dominated small pools. This is not surprising, because pool size and depth were positively correlated ($r = 0.34$). However, there are some species that tended to dominate large, but relatively shallow pools more often than most species (e.g., *Castilleja campestris*) and others that tended to dominate relatively deep and small pools (e.g., *Gratiola ebracteata*).

Rare Plant Species

Two rare plant species were found: *Legenere limosa* and *Downingia pusilla*. Neither species is listed by the federal government or State of California as threatened or endangered, but *L. limosa* is considered rare, threatened, or endangered in Cali-



□ Modesto ○ Riverbank △ Laguna ◇ Mehrten

FIGURE 5. Ordination of vernal pools by the first and third canonical variables of a canonical discriminant analysis of vernal pool plant species abundance scores for four geomorphic surfaces.

fornia and elsewhere by the California Native Plant Society (CNPS), and CNPS considers *D. pusilla* rare, threatened, or endangered in California, but more common elsewhere (Skinner and Pavlik, 1994). Each species was found in four pools. *D. pusilla* was found in 3 pools on the Laguna Formation and 1 pool on the Modesto Formation (2 individuals). *Legenere limosa* was found in 3 pools on the Modesto Formation and 1 pool on the Riverbank Formation. Pools with *L. limosa* tended to be deeper and larger than the average pool, but pools with *D. pusilla* did not differ from average in area or depth (Table 4).

Large Branchiopods

Three large branchiopods were found: the notostracan *Lepidurus packardi* (Vernal Pool Tadpole Shrimp), and the anostracans *Branchinecta lynchi* (Vernal Pool Fairy Shrimp) and *Linderiella occidentalis* (California Linderiella). These anostracan species were found in the egg stage and in the active stage. *Lepidurus packardi* was reliably identified in the active stage only. *Lepidurus packardi* is listed as endangered and *B. lynchi* is listed as threatened by the U.S. Fish and Wildlife Service. *Linderiella occidentalis* has no legal protection status.

Active *L. packardi* were found in 23 pools, 21 on the Riverbank Formation (6% of Riverbank Formation pools) and 2 on the Modesto Formation (1% of Modesto Formation pools; Fig. 8). No active *L. packardi* were found in Laguna or Mehrten Formation vernal pools. The distribution of active *L. packardi* differed significantly among geomorphic surfaces ($\chi^2 = 6.0$; $df = 3$; $P = 0.01$).

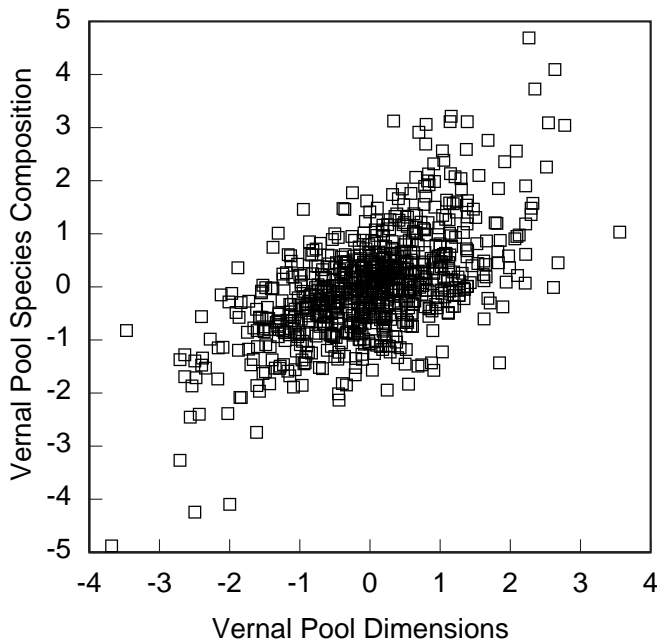


Figure 6. Ordination of vernal pools by the first canonical variable for vernal pool dimensions (pool area and depth) and the first canonical variable for species composition (species abundance scores) derived from a canonical correlation analysis.

Active *B. lynchi* were found in 131 pools, in 13% of Modesto Formation pools, and in approximately 20% of Laguna and Riverbank Formation pools, no active *B. lynchi* were found in Mehrten Formation pools (Figure 8). Geomorphic surfaces did not differ significantly in *B. lynchi* frequency ($P = 0.14$). *Branchinecta lynchi* eggs were found in 127 of 804 sampled pools (15.8%). Frequencies did not differ significantly among geomorphic surfaces ($P = 0.59$), but the frequency in Mehrten Formation pools (10.8%), tended to be lower than in the Modesto, Riverbank and Laguna Formation pools (16.9, 16.8 and 15.4%, respectively). The probability of finding active *B. lynchi* was not significantly different between pools with eggs and pools without eggs ($P = 0.17$).

Active *L. occidentalis* were found in 185 pools (Figure 8). The frequency in Modesto and Riverbank Formation pools (29%) was higher than the frequency in Laguna Formation pools (18%). No active *L. occidentalis* were found on the Mehrten Formation. The geomorphic formations were significantly different in frequency of active *L. occidentalis* ($\chi^2 = 10.7$; $df = 3$; $P = 0.005$). *Lindieriella occidentalis* eggs were found in only 7 pools. This number was considered too small for statistical analysis.

Logistic regression showed that the frequency of active *L. packardii* occurrence was dependent on pool area, but not on pool depth (Table 5). *Branchinecta lynchi* actives and eggs tended to occur more frequently in deeper pools than in shall-

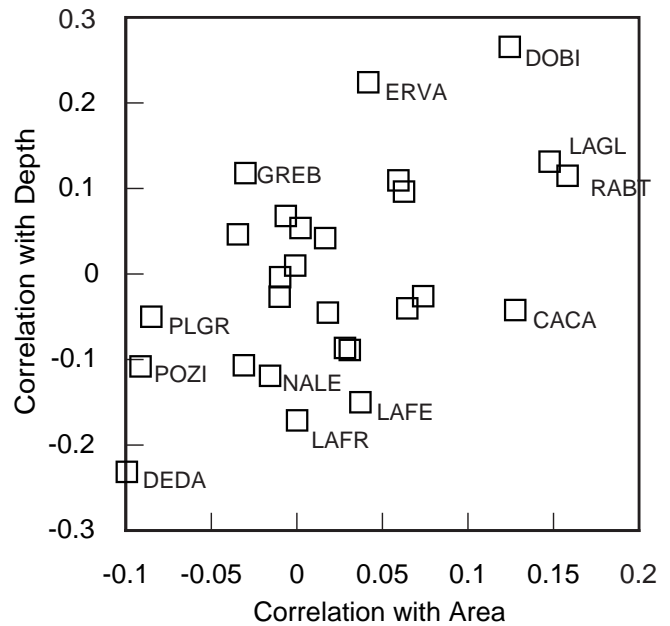


Figure 7. Partial canonical correlations with pool depth and area for vernal pool plant species that occurred in more than 50 vernal pools. Acronyms for selected species: CACA = *Castilleja campensis*, DEDA = *Deschampsia danthonioides*, DOBI = *Downingia bicornuta*, ERVA = *Eryngium castrense*, GREB = *Gratiola ebracteata*, LAFE = *Layia fremontii*, LAFR = *Lasthenia fremontii*, LAGL = *Lasthenia glaberrima*, NALE = *Navarretia leucocephala* ssp. *leucocephala*, PLGR = *Plagiobothrys greenii*, POZI = *Pogogyne zizyphoroides*, RABT = *Ranunculus bonariensis* var. *trisepalus*.

low pools (Table 5). Active *B. lynchi* frequency was negatively related to pool area, indicating that *B. lynchi* tended to occur more frequently in smaller pools than in larger pools (Table 5). Active *L. occidentalis* occurred more frequently in deeper pools than in shallow pools, but showed no significant relationship with pool area.

DISCUSSION

In spite of the physical and biotic complexity of vernal pool ecosystems a relatively small number of physical parameters may explain a considerable portion of the variation in biological diversity. This study considered just two physical parameters, maximum pool depth and surface area, because these variables can be measured relatively quickly. Several other parameters should be investigated if one were to fully understand the determinants of biological variation. However, the measurement of other relevant physical factors is more time consuming and complicated, or may even be impossible without excavation.

Vernal pool depth and area have important consequences for the hydrologic regime of vernal pools, including duration of

TABLE 4. Characteristics of vernal pools with rare plant occurrences and all vernal pools. Values are means \pm 1 standard error.

Species	Area (in m ²)	Depth (in cm)
<i>Downingia pusilla</i>	299 (\pm 89)	20.8 (\pm 3.7)
<i>Legenere limosa</i>	2,533 (\pm 694)	33.0 (\pm 6.6)
All vernal pools	481 (\pm 42)	20.3 (\pm 0.3)

ponding and frequency of drying during the growing season. Other parameters that affect vernal pool hydrology, for example depth to the impervious soil horizon, soil texture and watershed area are likely to be important determinants of biological diversity too. Chemical attributes and climate can be expected to have an effect on macrocrustacean diversity in vernal pools as well (e.g., Belk, 1977; Eng et al., 1990; King et al., 1996).

In addition to physical and chemical parameters, land management history should be considered as a factor with potential effect on vernal pool biological diversity. Past human ground disturbance and history of grazing practices vary over the landscape at Beale Air Force Base and consideration of these factors is likely to refine the conclusions presented in this paper.

Vernal pool depth and area had an important effect on plant species composition, and the occurrence of fairy shrimp. These factors are generally highly correlated (e.g., King et al., 1996), but appeared to affect some biological parameters differentially. For example, depth had a positive effect, and area a negative effect, on the frequency of active *B. lynchi* occurrence. However, the effects of depth and area on plant species composition were in the same direction.

A number of vernal pool plant species may occur in well-defined depth ranges (Holland and Jain, 1984). Most likely, because they are adapted to the different hydroperiods that occur at different depths. Therefore, shallow pools will be dominated by different species than deep pools. Deep pools may have a higher plant species richness, simply because they include more depth ranges. Natural vernal pool landscapes have vernal pools of a variety of depths, and therefore, vary in species richness.

Deeper pools also tend to have a higher probability of macrocrustacean occurrence than shallow pools. For example, deeper pools tend to have a higher frequency of eggs and active specimens of *B. lynchi*, and a higher incidence of active *L. occidentalis*. Active *L. packardii* tended to occur at greater frequency in deep pools than in shallow pools, but this difference was not statistically significant.

King et al. (1996) suggest that *L. packardii* requires relatively deep pools to complete its relatively long life cycle because these pools have a longer hydroperiod than shallow pools. However, they found *B. lynchi* only in shallow pools, while Eng et al. (1990) report that this species occurs at a wide range of depths, from shallow sandstone depression pools to grassland vernal pools of varying size. The higher frequency of fairy shrimp in deeper pools at Beale Air Force Base might be the result of low temperature requirements for hatching found in *Branchinecta* species (Belk, 1977), and low temperature requirements for hatching and adult survival in *L. occidentalis* (Eng et al., 1990). Deep pools may be buffered better against the temperature fluctuations that occur in the relatively mild California winter.

TABLE 5. Coefficients for multiple logistic regressions of invertebrate occurrence on vernal pool area and depth.⁽¹⁾

Species (life stage)	Source	Estimate	SE ⁽²⁾	χ^2	P
a. <i>Lepidurus packardii</i> (active)	ln(depth)	1.04	0.57	3.38	0.07
	ln(area)	0.68	0.17	15.04	0.0001
b. <i>Branchinecta lynchi</i> (active)	ln(depth)	2.55	0.31	66.39	<0.0001
	ln(area)	-0.29	0.08	12.49	0.0004
c. <i>Branchinecta lynchi</i> (egg)	ln(depth)	0.56	0.25	5.20	0.02
	ln(area)	-0.01	0.08	0.01	0.9
d. <i>Lindieriella occidentalis</i> (active)	ln(depth)	3.14	0.31	101.84	<0.0001
	ln(area)	-0.08	0.08	1.08	0.29

⁽¹⁾ The logistic regression models are of the form $\ln(p/(1-p)) = \beta_0 + \beta_1 D + \beta_2 A$, where p is the probability of an invertebrate occurrence, β_0 is an intercept and β_1 and β_2 are coefficients (given in the table), and $D = \ln(\text{depth})$ and $A = \ln(\text{area})$. For example, for regression "a" the estimates for the coefficients are $\beta_1 = 1.04$ and $\beta_2 = 0.68$. Positive values for β_1 and β_2 represent positive relationships between depth or area, and the probability of an invertebrate occurrence, negative coefficients represent negative relationships.

⁽²⁾ SE = Standard Error

PATTERNS OF VERNAL POOL BIODIVERSITY AT BEALE AIR FORCE BASE

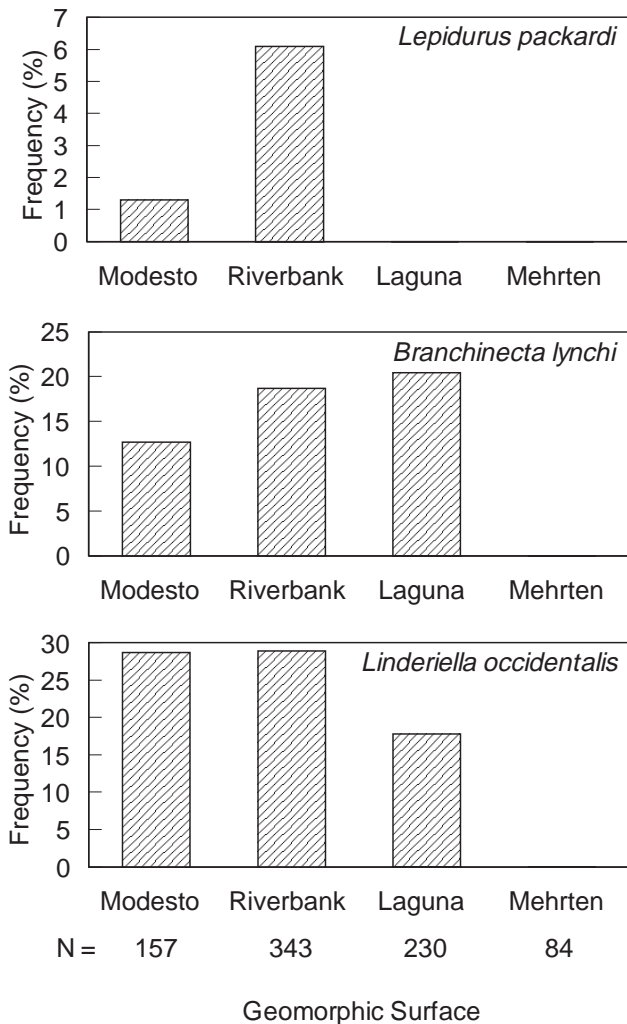


Figure 8. Frequency of active large branchiopod specimens in vernal pools on four geomorphic surfaces (formations). Frequencies are based on total of three samples for each vernal pool. N is the number of pools sampled.

Generally, the effects of vernal pool depth and area on biological variables were much more pronounced than the effects of geomorphic surface. Moreover, the differences among geomorphic surfaces could in part be attributed to differences in depth or area among geomorphic surfaces. Effects of factors other than depth and area that vary among geomorphic surfaces could not always be isolated with the statistical tools that I used, but several differences among geomorphic surfaces do not appear to be directly related to differences in vernal pool dimensions. In particular, the higher frequency of *L. packardi* and *B. lynchi* in Riverbank than in Modesto Formation pools is difficult to explain based on the difference in physical dimensions between the surfaces, because the opposite would be expected based on differences in pool dimensions between the surfaces.

Further studies of differences among geomorphic surfaces that include soil permeability, depth to the hardpan, solute concentrations and detailed analysis of the hydrologic regime may elucidate differences among geomorphic surfaces that could not be explained by the present analysis.

Effects of vernal pool depth and area, and geomorphic surface on biological diversity may differ between years. Holland and Jain (1984) found that vernal pools had a significantly lower plant species diversity in relatively dry years than in wet years. Similar effects can be expected for crustaceans. Crustacean species may even fail to hatch in shallow pools in dry years. The effect of a different level or seasonal distribution of precipitation on the differences among geomorphic surfaces or vernal pool dimensions is difficult to predict. Precipitation in the 1995/1996 wet season was above average and species richness and crustacean occurrences may have been higher than average.

The investigation of the environmental correlates of variation in biological diversity, can help design conservation strategies. The differences in plant species composition and large branchiopod occurrences among geomorphic surfaces suggest that conservation strategies should aim to preserve pools on different geomorphic surfaces. Furthermore, vernal pool size and depth appear to have an effect on plant species richness and rare plant and crustacean occurrences. Deeper pools have a higher probability of *Legenere limosa* and crustacean occurrences, and higher plant species richness. The data collected in this study suggest that deeper pools have on average a higher biological diversity than shallow pools and therefore should receive special attention in conservation planning. In spite of their lower plant species richness and crustacean occurrences, shallow pools differ ecologically from deep pools. This is evident, for example, from the different sets of dominant plant species.

The natural variation in depth related species diversity has implications for vernal pool creation projects. Vernal pools created to compensate for the loss of pools by human disturbance tend to be made relatively deep, because “success” criteria often require a certain minimum plant species diversity or minimum number of crustacean occurrences. This practice does not recreate the natural variability of the impacted landscape. When the goal of vernal pool conservation or creation is the maintenance of biological diversity, then both deep and shallow pools should be preserved or created.

In addition to vernal pool dimensions and geomorphic surfaces, resource management history should be considered in designing a vernal pool conservation plan. Certain areas may have a relatively low species richness and low occurrence of rare species because the habitat has been degraded by past management practices. The species diversity potential of such sites can

be suggested by the size or depth distribution of the pools, and the geomorphic surface. Areas that are candidates for restoration of vernal pool habitat can be identified based on his information.

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