

A Comparison of Pollination Interactions in Natural and Created Vernal Pools in the Santa Rosa Plain, Sonoma County, California

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ABSTRACT. Pollination interactions in natural and created vernal pools were compared at the Alton Lane mitigation site, in the Santa Rosa Plain, Sonoma County, California four years after artificial pool creation and translocation of *Blennosperma bakeri* populations. Floral visitation, seed production, and floral patch attributes of *B. bakeri* were measured in eight created pools and eleven natural pools. The Alton Lane mitigation site supported a densely packed mosaic of approximately 50 natural, created, and restored vernal pools. *Blennosperma bakeri* floral patches in created pools were significantly larger in area, but floral density was significantly lower in created pools during the period of observation. Seed production of *B. bakeri* heads was slightly greater within created pools and was negatively correlated with floral density. The floral visitation rate by bees and flies combined was not significantly different in natural and created *B. bakeri* patches. Analysis of floral visitor composition revealed that floral visitation in created vernal pools was significantly fly-dominated, with bees uncommon, whereas visitation in natural pools was more equitable between bees and flies. Common floral visitors included native bees and a specialist bee, *Andrena blennospermatis*, as well as empidid and syrphid flies. Visit frequencies of bees and flies were not significantly influenced by floral patch area, density, or seed set. Four years post-construction, native bee utilization of *B. bakeri* patches was dissimilar between natural and created pools. Findings suggest that four bee generations may not be long enough for pollination interactions to be fully established in created vernal pool landscapes.

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INTRODUCTION

Vernal pool habitats are ephemeral wetland habitats characterized by seasonal, rain-fed pools that form annually as a result of water ponding over a poorly draining substrate layer (Keeley and Zedler, 1998). The distinctive flora associated with California vernal pool landscapes is species-rich, with many endemic and endangered species adapted to the seasonal extremes of winter/spring inundation and summer drought. Accelerating agricultural and urban/suburban development in California over the past century has resulted in the loss of 90-95% of historical vernal pool habitat (Hol-

land, 1978, 1998). Recent expansion of orchards and vineyards is thought to account for about 30% of vernal pool habitat losses in the Great Valley during 1997-2005 (Holland, 2011). Remaining natural vernal pool landscapes, such as those within the Santa Rosa Plain in Sonoma County, California are the foci of long-term conservation efforts that involve complex issues of mitigation, restoration, and preservation of vernal pool habitats (Jensen and Emery, 2009).

Sonoma sunshine, *Blennosperma bakeri* Heiser (Asteraceae), is one of several endangered vernal pool plant species endemic to the Santa

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Rosa Plain. It is an annual that typically flowers in early spring and tends to grow within shallow pools (Ornduff, 1963, 1964). Although Ornduff (1963, 1964) found that *B. bakeri* was predominately outcrossing, recent studies suggest that some selfing may occur (Leong, unpublished data; Sloop and Brown, 2009). An oligolectic bee, *Andrena blennospermatis*, various other native bees, flies, and beetles are common floral visitors to *B. bakeri* (Davis, 1998; Thorp, 1990, 2007; Thorp and Leong, 1995, 1998). Habitat destruction has led to translocation of many *B. bakeri* populations to mitigation sites that often contain natural and artificially created vernal pools. Translocation of endangered plant populations is a controversial mitigation practice (Howald, 1996; Elam, 1998; Hubbert et al., 2001) that has been employed throughout vernal pool regions in California. One reason why translocation of endangered plant species is not favored by conservation scientists is because essential ecological interactions that contribute to the long-term success of vernal pool plant populations are not likely to be translocated along with seed or plant propagules. Consequently, translocated populations may lose a large network of ecological interactions; some of these interactions, might be regained, depending on the characteristics of the newly created vernal pool receptor site.

This study examined the status of one ecological interaction, pollination, in natural and created vernal pools at a *B. bakeri* mitigation site four years after artificial pool creation and translocation of *B. bakeri*. Comparative investigations of species interactions in natural and created vernal pool habitats are rarely done (Leong, 1994; Leong and Bailey, 2000; Schiller et al., 2000); but these types of studies are necessary in order to evaluate potential functional differences between natural and created habitats (Fisher, 1998). In this study, I addressed the following questions: 1) How similar are *B. bakeri* floral patches in natural

versus created pools in terms of patch size, patch isolation and floral density? 2) Does seed reproduction differ between populations in natural and created pools? 3) Does pollinator visitation frequency differ between *B. bakeri* in natural and created pools? 4) Are the kinds of pollinator taxa similar between natural and created pools?

STUDY SITE

The Alton Lane mitigation site is located in Santa Rosa, Sonoma County, California (38°28.3'N, 122°46.6'W). This site historically supported a natural vernal pool landscape, but it is now composed of a mosaic of natural, created, and restored vernal pools and swales. Packing of created pools into the natural grassland matrix (Leidy and White, 1998) has resulted in a much greater total pool density at this site than before mitigation actions occurred. At the time of this study, in spring 1993, there were approximately 50 pools and swales within this 16 hectare site, about half of which were created. The created pools sampled in this study were constructed in 1989 as compensatory mitigation for the destruction of nearby populations of *B. bakeri* and *Lasthenia burkei*. In 1989, 11 new vernal pools were created and 9 pre-existing pools or swales were variously restored or enhanced (Figure 1). More pools were constructed post-1989 as part of separate mitigation agreements. Created pools were excavated in the upland grassland matrix and spatially integrated with existing natural vernal pools. Created and restored pools were planted with either seeds or live plants translocated from *B. bakeri* populations that were approximately 1.6 km from the Alton Lane mitigation site. Currently, this site supports sizeable populations of *B. bakeri*. A citizen science project that monitors *B. bakeri* at the Alton Lane site reported population estimates in the range of 998,500-2,472,000 in 2009-2010 (Laguna de Santa Rosa Foundation, 2011).

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FIGURE 1. An aerial photograph of the Alton Lane mitigation site (circa 1988-1989). A subset of the natural vernal pools and swales shown, and a subset of the large created pools visible in the foreground, were examined in this study. Additional created pools were constructed by the time this study was conducted in 1993. Photograph courtesy of California Department of Fish and Game, Plant Conservation Program.

METHODS

Floral patches or populations of *Blennosperma bakeri* within eleven natural vernal pools and eight created pools were sampled in April-May 1993. A total of nineteen floral patches were studied, one patch per pool. Estimates of patch size and distance to the nearest patch (patch isolation) were determined by measuring patch dimensions and distances using both field tapes and measured paces. Patch boundaries were discrete except in a few cases, in which plants 2 m or more distant from the main body of the patch were not considered part of the patch.

To estimate seed production, 12 mature seed heads were collected randomly from *B. bakeri* patches within natural and created pools during 19-21 April 1993. Each head was collected from a separate plant. These pools were chosen because the *B. bakeri* patches within these pools were at similar stages of flowering phenology and because the natural and created

pools were located in similar areas within the study site. Percent seed set per head (capitulum) was calculated as the ratio of mature seeds to total ovules. Seed set data were arcsine transformed prior to analysis with an unpaired t-test. Floral density estimates were made in early April, at the beginning of the flowering season, and one month later in early May. Early floral density estimates were taken at the same time as floral visitation observations. The number of flowering heads within randomly located 0.5 m by 1.0 m plots was estimated by counting four 0.5 m x 0.125 m belt transects within the plot; the mean of these values was then multiplied by eight. Late floral density estimates were taken by recording floral density categories (1-25, 26-50, 51-75, 76-100, >100 flowering heads) in seven 0.25 m x 0.25 m plots randomly located within each patch. The early floral density measurements estimated local floral density in the same plots where pollinator visitation was measured, whereas late floral density measurements reflected a patch level estimate of

floral density.

Pollinator visitation to *B. bakeri* heads was recorded over seven days in early April within randomly located 0.5 m x 1 m plots, a subset of which was also used for early floral density estimates. Floral heads within each plot were observed for 12 minutes, between the hours of 1000 and 1400. A total of 45 observation periods were recorded in 45 plots in natural and created pools, which corresponds to 2 or 3 replicate periods per pool. A visit to a flower head was recorded if the insect visitor landed on the flower and contacted the floral reproductive structures (anthers and stigmas). On most days, each visit observation period within a natural pool was systematically followed by an observation period within a created pool. Visit frequency values were square root transformed prior to analysis with an unpaired t-test. On visitation days, floral visitors were netted on *B. bakeri* flower heads; subsequently, bee specimens were later identified by Dr. Robbin Thorp, University of California, Davis.

RESULTS

Blennosperma bakeri patches in created pools were significantly larger than those in natural pools (Mann-Whitney U, $Z = -2.3$, $p = 0.021$, Figure 2). The median patch area in created pools was 82.2 m², while the median patch area in natural pools was 20.3 m². However, floral patch isolation was similar between created and natural pools (Mann-Whitney U, $Z = -1.5$, $p = 0.13$). The median patch isolation distance for created pools was 16.5 m, while the median patch isolation distance for natural pools was 12.9 m.

Floral density was significantly lower in created pools during the periods of observation. Early in the *B. bakeri* flowering season, the median floral density was 176 flowers/0.5 m² in created pools, in comparison with a me-

dian density of 320 flowers/0.5 m² in natural pools (Mann-Whitney U, $Z = -2.9$, $p = 0.0038$). A floral census conducted one month later that recorded density categories revealed a similar pattern (Figure 3). The majority of plots in natural pools were in the two highest density categories (≥ 76 flowers/0.0625 m²) whereas the majority of plots within created pools were in the two lowest density categories (≤ 50 flowers/0.0625 m²) (Mann-Whitney U, $Z = -3.02$, $p = 0.0026$). For all pools, floral density was negatively correlated with patch area, for early (Spearman Rank, $Z = -2.27$, $p = 0.023$) and late (Spearman Rank, $Z = -2.0$, $p = 0.045$) density estimates.

Seed production of *B. bakeri* capitula was slightly higher in created vernal pools ($t = 2.18$, $p = 0.031$, Table 1), with a mean percent seed set of 53.0 ± 0.16 S.E. in created pools and a mean percent seed set of 48.9 ± 0.14 S.E. in natural pools. Mean percent seed set in all pools was negatively correlated with floral density, but only late in the flowering season (Spearman Rank, $Z = -2.66$, $p = 0.0077$). Mean percent seed set in all pools was not correlated with floral patch area (Spearman Rank, $Z = 0.79$, $p = 0.43$).

A total of 583 floral visits were observed to *B. bakeri* within created and natural vernal pools. The predominant floral visitors to *B. bakeri* were various kinds of native bees and flies (Table 2). Empidid flies were the most common floral visitors observed. Floral visitation was highly variable by both bee and flies (Figures 4 and 5) and was characterized by many observation periods with zero visits from either bees (51%) or flies (24%). *Blennosperma bakeri* in created and natural vernal pools received similar levels of floral visitation by bees and flies combined ($t = -0.99$, $p = 0.34$). The average combined visit frequency in plots placed in created pools was 11.42 ± 5.7 S.E. visits per observation period while the average combined visit frequency in plots

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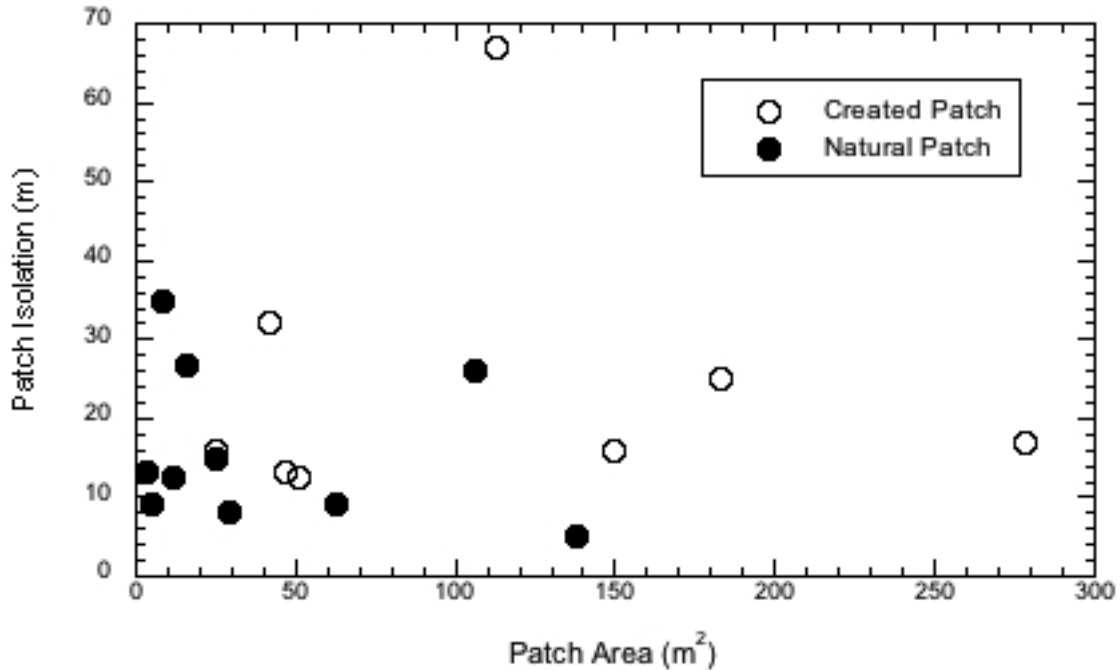


FIGURE 2. Floral patch area and distance to nearest *B. bakeri* patch (patch isolation) for the eight created (unfilled circles) and eleven natural vernal pools (filled circles) examined in this study. One natural pool is not shown due to missing data.

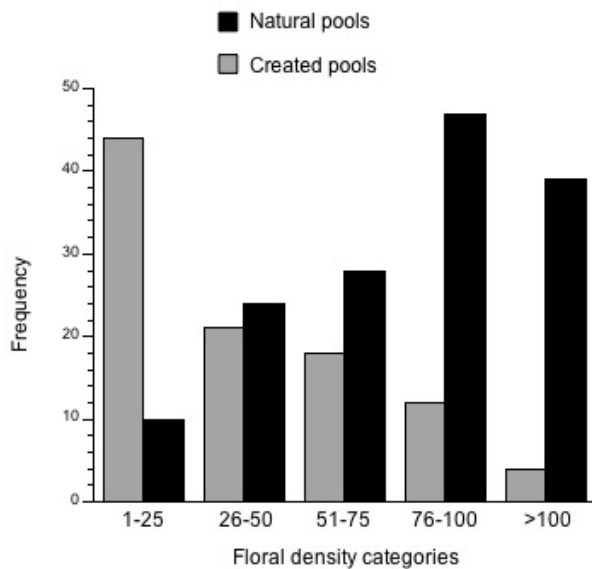


FIGURE 3. *Blennosperma bakeri* floral density categories recorded within 0.25 m by 0.25 m plots in natural and created vernal pools. Black bars denote densities in natural pools and gray bars denote densities in created pools.

placed in natural pools was 15.21 ± 3.5 S.E. visits per observation period. Analysis of floral visit species composition (Table 3) revealed that *B. bakeri* floral visitation in created vernal pools was highly fly-dominated, with bees uncommon, whereas visitation in natural pools was more equitable between bees and flies ($\chi^2 = 40.8$, $p < 0.0001$). In natural pools, the total number of bee visits observed was more than four times greater than those observed in created pools. In all *B. bakeri* patches, floral visitation by flies comprised almost two thirds of all visits observed (65.5%). Combining all pools, mean bee visit frequency was not correlated with mean fly visit frequency (Spearman Rank, $Z = 0.43$, $p = 0.66$).

Mean visit frequencies of bees and flies were not influenced by floral patch attributes. In all pools, floral patch area was not correlated with visitation by bees (Spearman Rank, $Z = 1.11$, $p = 0.27$) or flies (Spearman Rank, $Z = -1.42$, $p = 0.16$). Similarly, mean percent seed

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TABLE 1. Seed production of *B. bakeri* in eight created and eleven natural vernal pools at the Alton Lane mitigation site in April 1993. Mean values per pool are given below (n = 12). Percent seed set was slightly higher in created vernal pools (t = 2.18, p = 0.031)

Pool ID	Type	# of mature seeds/head	Total # of ovules/head	% Seed set
1N	Created	4.5	9.08	49.5
2N	Created	5.3	9.75	54.8
4N	Created	5.5	9.17	61.2
5N	Created	4.58	10	45.9
6N	Created	4.75	9.83	48.7
7N	Created	5.17	9.58	55.3
8N	Created	5.08	9.58	52.7
10N	Created	5.42	9.83	56.1
3	Natural	4.42	10.5	42.0
4	Natural	4.92	9.91	51.7
5.1	Natural	4.58	10.25	45.2
5.2	Natural	4.5	9.83	46.5
15	Natural	5.08	9.17	55.9
20	Natural	4.75	8.58	54.8
23/10	Natural	4.75	9.92	48.9
25	Natural	5.08	9.67	53.4
G.1	Natural	4.08	10.08	40.6
G.2	Natural	4.0	8.83	44.5
H	Natural	4.58	8.45	54.3

set of floral patches was not associated with mean visit frequencies of bees (Spearman Rank, $Z = -0.058$, $p = 0.95$) or flies (Spearman Rank, $Z = 0.18$, $p = 0.85$). Floral density of *B. bakeri* patches early in the season (when visit observations were conducted) did not influence mean visit frequencies of bees (Spearman Rank, $Z = 1.43$, $p = 0.15$) or flies (Spearman Rank, $Z = 0.80$, $p = 0.42$).

DISCUSSION

At the Alton Lane mitigation site, four years post-creation, *B. bakeri*-pollinator interactions in natural versus created vernal pools were

significantly different in terms of the kinds of insects that visit its flowers. Results indicate that *B. bakeri* flowers in created pools were visited primarily by flies, with few bee visits, while *B. bakeri* flowers in natural pools were visited more equitably by native bees and flies. The more than four-fold reduction in the total number of bee visits to flowers in created pools resulted in a shift to a fly-dominated visitor assemblage. Overall floral visitation frequency, however, was similar between natural and created pools. The difference in the floral visitor assemblage cannot be explained by variation in floral patch size or density; these variables were not correlated with bee or

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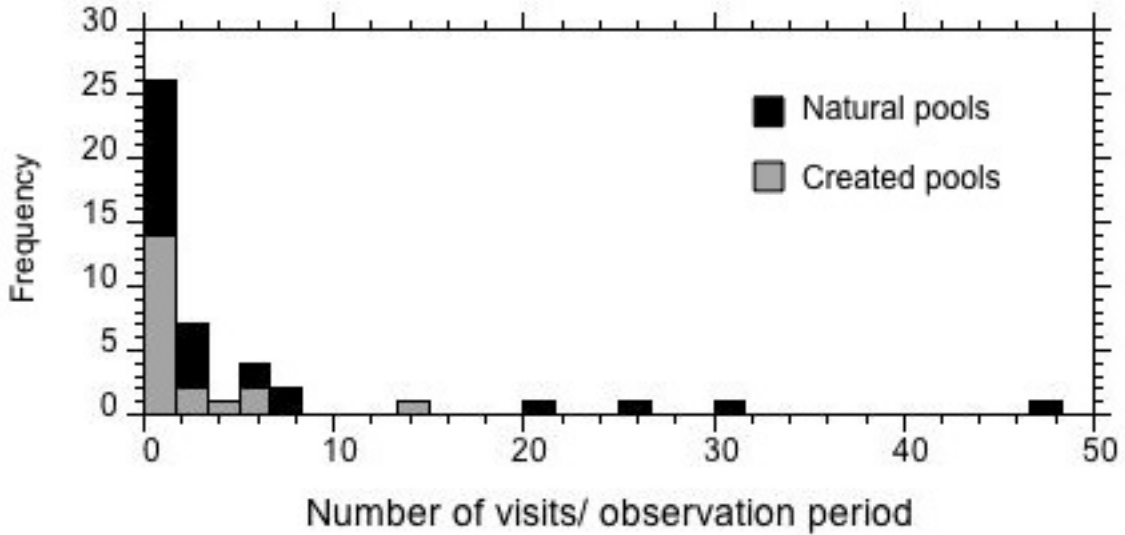


FIGURE 4. Frequency of the number of bee visits observed in *B. bakeri* visitation-plots in natural and created vernal pools during twelve-minute observation periods. Black bars denote visits in natural pools and gray bars denote visits in created pools. Total frequency of the observed number of bee visits from natural and created pools combined is shown by the height of each bar.

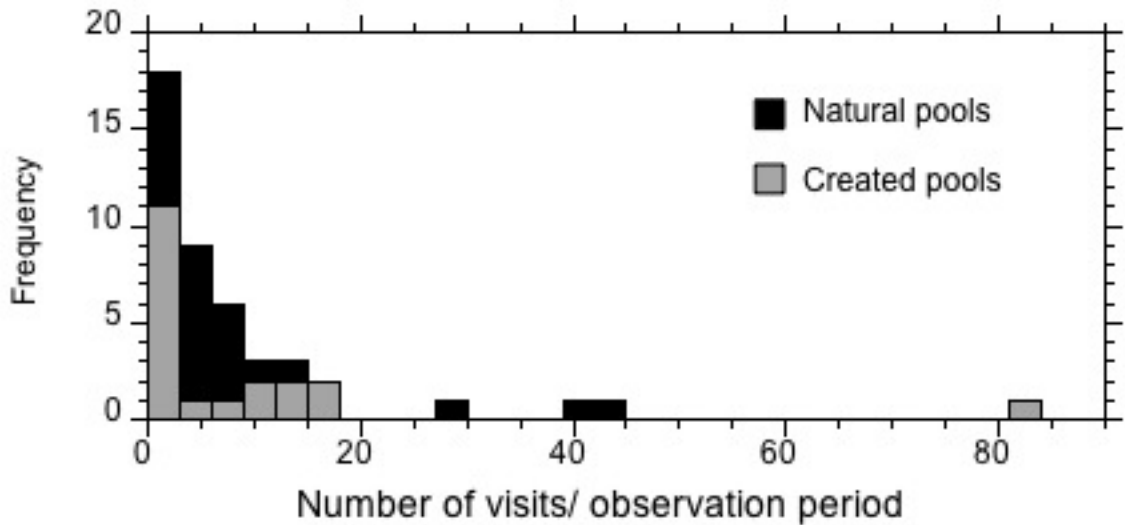


FIGURE 5. Frequency of the number of fly visits observed in *B. bakeri* visitation-plots in natural and created vernal pools during twelve-minute observation periods. Black bars denote visits in natural pools and gray bars denote visits in created pools. Total frequency of observed number of fly visits from natural and created pools combined is shown by the height of each bar.

fly visitation. The small, but statistically significant difference in *B. bakeri* seed production within natural and created vernal pools is not explained by the larger differences in floral visitation. The greater seed production per capitulum in created pools is likely explained

by the significantly lower floral densities in created pools. For all pools, floral density was found to be negatively correlated with seed production.

Not surprisingly, the findings of this study are

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TABLE 2. Floral visitors of *B. bakeri* at the Alton Lane mitigation site in April 1993.

HYMENOPTERA (BEES)	
	<i>Andrena (Diandrena) blennospermatis</i>
	<i>Andrena (Diandrena) cuneilabris</i>
	<i>Andrena (Hesperandrena) pulverea</i>
	<i>Andrena (Simandrena) angustitarsata</i>
	<i>Andrena (Simandrena) pensilis</i>
	<i>Halictus ligatus</i>
	<i>Lasioglossum titusi</i>
DIPTERA (FLIES)	
	Empididae
	Syrphidae
	Rhagionidae
	Anthomyiidae
	Conopidae
COLEOPTERA (BEETLES)	
	Miscellaneous
LEPIDOPTERA (BUTTERFLIES/MOTHS)	
	Miscellaneous

in some ways similar, but in other respects differ, from previous comparisons of *Blennosperma nanum* in natural and constructed vernal pool habitats (Leong, 1994). Leong (1994) found that *B. nanum* seed production, pollinator visitation rate, and the number of visitor taxa was significantly lower in potted plant arrays placed in a created vernal pool site (no natural pools or *B. nanum* populations were present) than in arrays placed in a natural vernal pool site. Pools were created six years prior to the experiments done by Leong (1994). Similar to the present study, a fly-dominated visitor assemblage (mostly empidid flies) to *B. nanum* arrays was found at the created site and at locations ≥ 1 m from the edge of a *B. nanum* patch at the natural vernal pool site (Leong 1994). Concordant with this study, Leong (1994) found that andrenid bee visitation was more frequent within natural patches of *B. nanum* and that seed set of *B. nanum* was not explained by differences in

floral visitation. In contrast to the present study, a study of the pollination of endangered *Pogogyne abramsii* in natural and created vernal pools in San Diego (Schiller et al., 2000), concluded that pool type (natural vs. created) did not influence pollinator visitation or effectiveness. Schiller et al. (2000) conducted their study one year after artificial pools were created in an area that supported natural vernal pools.

In this study, *Andrena blennospermatis* was observed infrequently foraging on *B. bakeri* in created pools, as were other andrenid and halictid bees (Table 2). Fewer bee visits to *B. bakeri* in created pools might be explained by the limited foraging ranges of these small bees (Thorp, 1990, 2007; Leong et al., 1995; Gathmann and Tscharntke, 2002; Emery, 2009) and/ or by proximity of nest sites to natural pools. Previous studies suggest that the typical scale of foraging within or between floral patches for small vernal pool bees (from the point of marking) is within 10 m, and rarely to 25 m (Thorp, 1990; Leong et al., 1995). If the majority of bee nest sites at Alton Lane were located near their natural host plant patches, as has been found in other studies (Rust, 1976; Thorp, 1990), and bees exhibited area-restricted foraging as was documented in previous studies, then relatively fewer andrenid visits would have been made to *B. bakeri* in created pools, which were 10+ m distant from other *B. bakeri* patches. One reason nest sites might have been closer to natural pools than created pools is that bees may exhibit fidelity to their natal nest site. Alternatively, it is possible that areas near created pools did not contain much suitable nesting habitat or that existing nests were destroyed in the process of pool construction. Nest site selection and nesting requirements are incompletely understood for these native bees (Rust, 1976; Thorp, 1990, 2007).

Within created vernal pools, *B. bakeri* floral

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TABLE 3. Total bee and fly visits observed within *B. bakeri* plots in natural and created pools at the Alton Lane mitigation site. Percentage values are calculated from row totals. Floral visitation was significantly fly-dominated in created vernal pools ($\chi^2 = 40.8$, $p < 0.0001$).

	Bee visits	Fly visits	Totals
Created pools	37 (17.5%)	174 (82.5%)	211
Natural pools	164 (44%)	208 (56%)	372
Totals	201 (34.5%)	382 (65.5%)	583

patches were larger and less dense than those within natural pools and swales at the Alton Lane mitigation site. Even larger-sized created vernal pools and *B. bakeri* floral patches than those examined in the present study were constructed at the Alton Lane site between 1990-1993. Therefore, the difference in *B. bakeri* patch size between created and natural pools reported in this study is undoubtedly conservative. The trend of “super-sized” created vernal pools at this site indicates that most areas at this site do not possess landscape features at the same spatial scale as in natural vernal pool landscapes. Lower floral and plant densities within created pools have been reported in other comparative studies of vernal pool mitigation sites. Schiller et al. (1990) found *Pogogyne abramsii* floral densities and plant densities were lower in created versus natural vernal pools. The mean percent cover of another Santa Rosa Plain endemic, *Limnanthes vinculans*, was lower in created pools, and higher in natural pools and swales (Jensen et al., 2009). Lower plant densities in created pools might be caused by a sparse seed bank and/or low initial translocation densities, or by suboptimal hydrological or soil conditions. At Alton Lane, the novel spatial characteristics of mitigated areas may have affected foraging/visitation activities by andrenid bees. For instance, the larger *B. bakeri* patch sizes in created pools may have encouraged a greater amount of intrapatch foraging

and less interpatch foraging by bees.

In conclusion, four years post-construction, some aspects of *B. bakeri* pollination were similar in natural and created vernal pools, but floral visitor assemblage clearly differed from those in natural pools. Native bee utilization of *B. bakeri* patches was dissimilar between the two pool types, but overall floral visitation rate and seed production were similar. *Blennosperma bakeri* seed production may be somewhat buffered from fluctuations in pollinator visitation as some selfing may occur (Leong, unpublished data; Sloop and Brown, 2009). Interestingly, at the same site, Leong and Bailey (2000) also found differential utilization of *B. bakeri* patches in natural and created pools by a flower-feeding thrips herbivore, *Frankliniella minuta*.

Taken together, these results suggest that small, movement-limited insects had not yet established typical *B. bakeri* utilization patterns in created vernal pools at the time of this study. Perhaps it is unrealistic to expect that typical patterns of plant utilization could develop in created vernal pool landscapes over the short span of four bee generations. It is unclear whether the results of this “snapshot” comparison of pollination function represent a point along a stable, continuing trend, or whether the differences captured by this study are a glimpse of a more variable ecological in-

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teraction that fluctuates from year to year. Additional comparative studies of pollination at long-term vernal pool mitigation sites, such as Alton Lane (Gilmore et al., 2009), are needed to discern which of these scenarios is applicable.

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