

CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

NO ALLEE EFFECTS IN LYON'S PENTACHAETA, A FEDERALLY LISTED  
ENDANGERED SUNFLOWER

A thesis submitted in partial fulfillment of the requirements  
for the degree of Master of Science in Biology

By

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## ABSTRACT

### NO ALLEE EFFECTS IN LYON'S PENTACHAETA, A FEDERALLY LISTED ENDANGERED SUNFLOWER

By

Jocelyn R. Holt

Master of Science in Biology

Potential Allee effects were investigated in *Pentachaeta lyonii*, an annual Asteraceae that is listed as federally endangered. Since *P. lyonii* is self-incompatible and has no evident seed dormancy, pollination service is essential for persistence. Observations of floral visitors showed that insect composition varied by site, year, and over the flowering season. The most common visitors were the bee-flies *Lepidanthrax* sp. and *Paravilla* sp. and the bee *Ashmeadiella californica* subsp. *californica*. There were also late-season peaks of the bee-fly *Exoprosopa doris* and bee *Exomalopsis* sp. These generalist pollinators allowed ample pollination for *P. lyonii*. The absence of Allee effects was further supported by there being no difference in seed production between open-pollination and hand-augmentation treatments within patches. In 2008 there was a proportional increase in per-capita visitation rates with increasing density. Flower heads in low density quadrats did not suffer a significant reduction in seed production compared to flower heads in more dense quadrats. Flowering *P. lyonii* in pots were placed in patches of various densities and at distances up to several meters from a patch. The

percent of quadrats visited was higher inside a patch (69%) than outside a patch (16%), but seed set was not reduced by being placed outside a patch. Visitation to lone potted plants was equal to or greater than visitation experienced by potted plants inside patches, possibly because an individual flower head is less attractive when surrounded by conspecifics. Isolated plants at one site were visited more by melyrid beetles and *Ceratina* bees than the visitors to patches of flowers. These results indicate that other factors such as habitat loss and competition with non-native plants are likely responsible for populations not expanding in size and in some cases declining.

Keywords: Allee effect, *Pentachaeta lyonii*, endangered species, pollination, California endemic

## INTRODUCTION

The coastal sage scrub community is a threatened ecosystem that is shrinking due to urban development (Davis et al. 1994; Minnich and Dezzani 1998; Rundel 2007) and from type-conversion to a vegetation dominated by non-native annuals (including *Bromus madritensis*, *Bromus hordeaceus*, *Bromus tectorum*, *Erodium botrys*, *Erodium cicutarium*, and *Centaurea melitensis*; D'Antonio and Vitousek 1992; Keeley 2004). As a result of habitat destruction and fragmentation, some populations of endemic species have become isolated. This brings up the question of whether such a species has populations at densities above the level needed to effectively reproduce.

The Allee effect addresses the dynamics of aggregations in sparse populations (Allee 1927; Allee and Rosenthal 1949; Stephens et al. 1999) and today has become associated with reproductive ability. It can be broken into component and demographic effects (Stephens et al. 1999; Gascoigne et al. 2009). A component Allee effect is defined as a positive relationship between an individual's fitness and population density or size (Gascoigne et al. 2009). Demographic Allee effects examine the positive relationship in an individual's fitness and how it contributes to the per capita growth of a population (Gascoigne et al. 2009). Successful matings at the individual level do not necessarily translate into increased population growth as stochastic events can result in offspring mortality (Courchamp et al. 1999; Gascoigne et al. 2009).

Allee effects have been identified in the generalized pollination system of *Senecio integrifolius*, where low density populations had decreased seed set (Widén 1993). Lamont et al. (1993) showed that small populations of *Banksia goodii* experienced reproductive stasis. In a more severe case, Groom (1998; 2001) noted that isolated

patches experienced pollen limitation and recorded patch extirpation of *Clarkia concinna* subsp. *concinna*, an annual herb with both generalist and specialist visitors. Identifying an Allee effect often informs conservation strategies for rare plants (Forsyth 2003).

These examples suggest a question for any given rare plant species that has recently undergone a demographic decline: have the populations of the rare species been forced into a level of sparseness that causes Allee effects?

*Pentachaeta lyonii* A. Gray (Asteraceae) is a federally-listed endangered species. This annual yellow composite occurs in grasslands surrounded by coastal sage scrub or chaparral (Plate 1). *Pentachaeta lyonii* along with other wildflowers, serve as a food source for generalist pollinators (Plate 2). In exchange for providing insects food, *P. lyonii* obtains cross pollination, which is necessary for it to set seed (Fotheringham and Keeley 1998).

In determining a conservation strategy for an endangered organism, it is important to understand all aspects of its life cycle (Caughley 1994). Previous studies have reported on various portions of the lifecycle of *P. lyonii*. Keeley (1995) did not find any evidence for seed dormancy or for fire cues stimulating germination, although seeds are thought to have the capacity to remain viable during extended dry spells (Fotheringham and Keeley 1998). Fotheringham and Keeley (1998) recorded heterospecific pollen on bees that visited *P. lyonii* thus supporting the idea that *P. lyonii* has a generalized pollination system. Pollinator efficiency was investigated by Braker and Verhoeven (1998), who found that one visit by a bee or bee-fly was enough to cause this composite head to set seed. Further research revealed that a small amount of pollen from the non-native *Centaurea melitensis* was found on bees that visited *P. lyonii* and the co-occurring native

aster *Deinandra fasciculata* also was not a strong pollen competitor (Braker and Verhoeven 2000). Finally, Moroney et al. (in press) documented the negative effects of competition by non-native plants on growth and flower production both in pots and in field experiments. Although different portions of the life cycle have been studied, the ability to set seed and whether seed production is density-dependent has been heretofore neglected. By understanding the role of density in *P. lyonii*'s ability to attract pollinators and then develop seeds, the primary reason for population declines can be identified and continued declines might be prevented.

The purpose of this study is to understand how density and isolation affect the pollination success of *P. lyonii* and how the number of seeds produced by an individual flower head is affected by these factors. Subsets of natural populations with various densities were observed for visitation rates, insect species composition, and seed production. Similar observations were made on potted plants placed inside a patch and at various distances from a patch. The questions addressed were: (1) How does insect composition vary depending on flower-head density? (2) How does pollinator visitation depend on patch density, temperature, site, and whether a plant is inside or outside a patch? (3) Does pollen transfer via hand-augmentation significantly increase seed set when compared to open-pollinated flowers? (4) Do plants in low-density patches or outside of a patch suffer decreases in seed production?

## METHODS

### Study System

*Pentachaeta lyonii* is endemic to southwestern California. In 1942, there were 43 populations of *P. lyonii* distributed among the Santa Monica Mountains, Simi Valley, Palos Verdes Peninsula, and Santa Catalina Island. In 2006, Pucci recorded plants living in only 21 populations, with populations on the Palos Verdes Peninsula and Catalina considered extirpated. Individuals on Santa Catalina Island were last officially documented in 1931 and were thought to have been introduced (Fotheringham and Keeley 1998), but a recent find (May 27, 2011) of approximately 112 individuals in a more remote site on Catalina suggests otherwise (personal communication with Sarah Ratay). The most recent presumptive extirpation was at Stunt Ranch in the Santa Monica Mountains, where no flowering individuals were seen since 1990, after an 8-year decline in the numbers of individuals, habitat alteration from gopher activity, and increases in non-native plants (U.S. Fish and Wildlife Service 1999). In 2008, Moroney (personal communication) observed individuals at Stunt Ranch, suggesting that *P. lyonii* has seed banks. Although habitat alteration and competition with non-native plants has been found to decrease growth and can cause extirpation (Moroney et al. in press), the U.S. Fish and Wildlife Service (1999) suggested that an inability to attract pollinators might contribute to the decline of *P. lyonii*.

*Pentachaeta lyonii* grows in dense clay soils that are often sparse in competitors, occurring amid a more vegetated matrix (Fotheringham and Keeley 1998). Individuals can be found growing in trails that receive moderate foot traffic and along trail edges. Closely co-occurring plants are also short-statured annuals, including *Linanthus*

*dianthiflorus*, *Cryptantha* sp., *Lasthenia chrysostoma* (formally *L. californica*), *Lupinus bicolor*, *Navarretia hamata*, *Deinandra fasciculata* (formally *Hemizonia fasciculata*), *Saltugilia splendens* (formally *Gilia splendens*), *Eriastrum sapphirinum*, *Plantago erecta*, and *Chorizanthe staticoides*. *Pentachaeta lyonii* raised in pots with potting soil and given ample water often grow four times taller than those in the field (personal observation), but the supposition that wild *P. lyonii* are confined to disturbed and sparsely vegetated areas primarily due to a lack of competitive ability has yet to be confirmed. Poor dispersal may also be a factor restricting new patch establishment and even contributing to population declines. New patches may be established only very rarely, and the overall increase in population size may be very slow.

In 2008 and 2009, populations at three sites near Thousand Oaks, California, were studied: Sidlee (0325061, 3787047 UTM), Kirsten Lee (0329184, 3778060 UTM), and Triunfo (0332072, 3778067 UTM). Each population was composed of many patches that varied in area and density. The sites differed in population size (estimated 26,333 individuals in 2009 at Sidlee; estimated 15,936 individuals in 2009 at Kirsten Lee; estimated 62,581 individuals in 2008 and estimated 3,431,826 in 2009 at Triunfo: survey methods based on Elzinga et al. 1998 modified by C. Brighman and J. Moroney; Appendix A). The populations also differed phenologically. In general, flowers bloom and senesce first at Sidlee, then flowering at Kirsten Lee begins overlapping with the tail end of individuals at Sidlee, and finally individuals at Triunfo flower with much of the season overlapping with Kirsten Lee (personal observation).

## Effects of Density on Visitation and Seed Set in 2008

In 2008 from March to June, insect visitation was studied in patches of *Pentachaeta lyonii* that varied in density. Quadrats of 1 × 1 m were haphazardly placed in patches and each quadrat contained between 2 to 270 open flower heads (mean = 43.4; SD = 48.61;  $n = 135$ ). Density was scored as the number of open flower heads in a quadrat (number of quadrats at Sidlee = 41; Kirsten Lee = 27; Triunfo = 67). Each visit by a likely pollinator was recorded in each quadrat for 15 minute survey periods between 10:00 a.m. and 4:30 p.m., the time of day when pollinator activity peaked in preliminary observations. The number of visits in 15 minutes was counted as the number of times an insect landed on a head and contacted disk flowers. Visits to flower heads by each insect in a quadrat were counted. The goal was to relate insect visitation to quadrat density, which was an estimate of patch density, thereby quantifying the minimum patch density necessary for pollination.

After the 15-minute visitor censuses, two flower heads were chosen in each quadrat to monitor seed set. The two heads were chosen to be comparable in size and blooming stage. Each was marked with a numbered tape tag. One was randomly assigned to be hand-augmented, while the other was assigned to be open-pollinated. A paintbrush was used to pick up fresh pollen from flower heads in the surrounding area that were shedding pollen, excluding the two focal heads. The paintbrush was checked to make sure it held yellow pollen. Then the paintbrush was touched to the stigmas of the hand-augmented head. The pollen donor's flower head was tagged with tape to prevent later use in a hand-augmentation or an open-pollination treatment. When the entire flower head began to wither, plants were covered with mesh bags (openings approximately 0.22

mm wide). The bags were tied to and supported by wooden sticks (approximately 2 mm in diameter). After the phyllaries began to dry, which took a few days to more than a week, seeds were collected. Each head was placed in its own Petri dish. Using a dissecting microscope, pappus was picked away so seed development could be scored. The number of developed seeds and the number of undeveloped “ovules” (either not fertilized or aborted) were counted. Seed set data were complete for 50 pairs of hand-augmented and open-pollinated heads (23 pairs at Sidlee, 11 pairs at Kirsten Lee, and 16 pairs at Triunfo). There were 24 additional cases in which only one head of a pair could be scored (6 single at Sidlee, 5 single at Kirsten Lee, and 13 single at Triunfo).

Ideally, the data on insect visitation would have been analyzed using a curvilinear regression. An Allee effect would have been indicated by an acceleration in visitation as density increased. However, censuses of 15 minutes yielded a dataset containing many zeros and a wide scatter. So, the analysis was broken down into three parts, and for this initial presentation of the data, sites were pooled. (1) A non-parametric Spearman’s rank correlation was calculated for visits across all densities. (2) Logistic regression addressed whether density affected if a plant was visited or not. (3) For those quadrats that did receive a visit, a model II regression on log-log transformed data was used to test whether the effect of density was allometrically above or below 1.00, i.e., accelerating or decelerating.

In a more complicated analysis, site and temperature were additional predictor variables available for statistical modeling. Temperatures were measured with a digital thermometer shaded by a wooden housing at the time of the visitor censuses. Unfortunately, temperature was not measured at the beginning of data collection for 21

censuses at Sidlee. For later censuses, field temperatures were correlated against temperature readings from the internet at  $r = 0.847$  ( $n = 113$ ; internet temperatures from [www.wunderground.com](http://www.wunderground.com)). Given this correlation, field temperatures were regressed onto internet temperatures. The missing field values were calculated as  $\text{temperature}_{\text{field}} = 6.638 + 0.991 \times \text{temperature}_{\text{internet}}$ . In the analysis that followed, the three predictor variables were temperature including substituted values,  $\log(\text{density})$ , and site used in a general linear model attempting to account for  $\log(\text{visitation}+1)$ . Log transformations were used to improve normality of residuals and linearity.

To compare hand-augmentation heads to open-pollination heads, a paired  $t$ -test was done. Pairing focused the analysis on treatment effects, setting aside variation among quadrats and differences among sites that do not interact with treatment. Seed development was squared to improve normality, so the dependent variable was  $\left[ \frac{\text{seeds}}{\text{seeds} + \text{ovules}} \right]^2$ . The differences were, then,  $[\text{seed set in the hand augmented head}]^2 - [\text{seed set in the open pollinated head}]^2$ , and the mean of the differences was subjected to the  $t$ -test.

No statistical difference was found between hand-augmentation and open-pollination treatments, so the average of the squared values for seed production was used in subsequent analyses. In cases where one of the two seed set values was missing, the other one was used instead of the average of the two. General linear modeling was used to test for predictors of seed set. Possible predictors included in the model were site, density, visitation, and temperature. The model was simplified in a stepwise manner excluding the predictor with the highest  $P$  value when  $P > 0.25$ .

## Measuring Pollination Services Using Potted Plants in 2009

In 2009, plants in pots were placed in the field to measure pollination services. Starting the previous November, *Pentachaeta lyonii* seeds were sown in flats filled with a 50:50 blend of potting soil and pumice. As young plants grew, they were transplanted individually in one-gallon pots filled with the same soil. Plants in pots that were about to flower were transported to the appropriate field population (the same population as the parent seed) as needed beginning in April. Each potted plant was allowed to acclimate for 2-3 days before being used to measure the pollination environment.

At the three sites, plants in pots were placed in quadrats of differing densities (2 to 455 flower heads) and at varying distances away from a patch. Potted plants with more than one open flower head were trimmed back to one flower head that was just opening, and the flower head was tagged. Potted plants were left in place until the flower head was fully open, which took 1-3 days. For pots in patches, density was measured as the number of open flower heads in a  $1 \times 1$  m quadrat surrounding the focal flower head, including the focal flower head. For pots not in patches, distance to the three nearest blooming *P. lyonii* plants was measured and averaged. There were 119 pots inside patches that varied from having 2 to 455 heads flowering (mean = 73.0; SD = 64.69). There were 53 pots positioned 1 to 5 m from naturally occurring *P. lyonii*, 40 pots that were 5.01 to 10 m from a patch, and 36 pots that were 10.01 to 18.2 m distant across all sites. For censuses done inside a patch, data on visits to the flower head on the potted plant were kept separate from number of visits to heads in the surrounding quadrat. Visitation to flower heads of potted plants was monitored for two sequential 15-minute visitor censuses. The study was done from April to July and the two sequential censuses were designated as a

replicate. Including censuses at all distances there were 64 replicates at Sidlee, 112 replicates at Kirsten Lee, and 72 replicates at Triunfo.

Plants were left in place until the corollas began to wither. Then the flower head and part of the branch was bagged until seeds had time to set, which took about 1-2 weeks. After flowering, potted plants were often moved to a shaded area while their seeds matured. This reduced the amount of watering needed. After flower heads senesced, a previously used plant with a new flower head was in some cases redeployed. Mature seeds were counted as in 2008, but “ovules” were not because maturing heads were collected at a less uniform stage. Without the ovule numbers, seed production in 2009 was merely the number of mature seeds without a divisor (this dependent variable is often used: Byers 1995; Årgen 1996; Wirth et al. 2011).

In 2009, 15-minute visitor censuses were done in pairs. This allowed for a model II ANOVA to quantify the similarity in results obtained from two back-to-back 15-minute censuses ( $n = 248$ ). Variance components were calculated.

Potted plants tested whether pollination was as likely to be effective as plants were placed farther and farther away from a patch. A model with multiple predictors cannot include density and distance because all the potted plants that were inside a patch would have had near zero distance to neighbors, whereas those outside a patch varied in terms of distance. Because of this non-independence, the two predictor variables were not used simultaneously.

Several analyses were done to look for effects of density or of distance on visitation. Two dependent variables were available for study: the number of visits to the focal flower head on the potted plant and the number of visits to all the flower heads in a

1 × 1 m quadrat including the focal head. As in 2008, the data included many zeros from censuses with no visits, so several types of analyses were done. (1) A simple 2 × 2 test of independence was done relating whether or not a visit was observed to whether or not the census was inside or outside a patch. This was not a per-capita test and did not take into account that inside a patch many more flower heads were often being watched than outside a patch. (2) For a more quantitative view, the number of visits was divided by the number of flowering heads under observation, making the data into per-capita visitation rates. Outside of a patch the denominator was 1, whereas inside a patch the denominator was a larger number. The rate of visitation was plotted against distance. An Allee effect would have shown up as a negative scatter. (3) A query similar to (1) was done looking at visits only to the focal flower head on the potted plant. (4) A query similar to (2) was done on visits only to the focal plant. (5) Studying whether or not any flower heads within a quadrat were visited, the variables temperature, density, and site were used as predictors in a multiple logistic regression. (6) The same multiple independent variables were modeled as possible predictors of whether or not the focal head on a potted plant was visited.

Seed production was analyzed in four ways. (1) Whether or not a head set any seed was subjected to a multiple logistic regression using the predictor variables density, number of visits to the potted plant during the two visitor censuses combined, temperature, and site. Terms were eliminated step-wise when  $P > 0.25$ . (2) For those heads that produced seed, the number of seeds was subjected to a general linear model involving the same possible predictors. (3) The likelihood of setting seed was examined

in relation to whether a plant was inside or outside a patch. (4) For the subset of potted plants that were inside a patch, seed number was also regressed on patch density.



PLATE 1. *Pentachaeta lyonii* plants and habitat (A) A *P. lyonii* individual on compact soil surrounded by dry grass. (B) A flower head. (C) Flower heads senescing. (D) A senesced head with pappus protruding from achenes. (E) A dense patch of *P. lyonii*. (F) A potted plant inside a patch; note wire enclosure that was used to prevent herbivory.



PLATE 2. The most common insect visitors to *Pentachaeta lyonii* (A) *Ashmeadiella californica* subsp. *californica* a small bee visitor with pollen on scopae of abdomen (B) The bee visitor *Exomalopsis* sp. is larger than the former bee and carries pollen on its legs (C) A *Ceratina* bee (D) *Lepidanthrax* sp. a short-tongued bee-fly (E) *Paravilla* sp. a short-tongued bee-fly similar in color and overlapping in size with *Lepidanthrax* sp. (F) *Exoprosopa doris* is a bee-fly with mottled wings that is larger than the previous bee-flies (G) *Copestylum* a syrphid hover-fly (H) A melyrid beetle; often seen on lone potted plants. (I) *Bombylius lancifer* a long-tongued bee-fly, not often observed and grouped with other Bombyliidea.

## RESULTS

### Insect Composition

A total of 5,720 insects (Apidae, Bombyliidae, Lepidoptera, Megachilidae, Melyridae, Syrphidae; Plate 2) were observed visiting 24,012 *Pentachaeta lyonii* flower heads at the three sites over the two flowering seasons. This means that in a given 15-minute census, the probability that a flower head would be visited was 0.238 visits/flower head, which extrapolates to 7.6 visits over 8 hours of a sunny day during which it might be assumed that any given stigma would have been receptive.

In 2008, the bee-fly group *Lepidanthrax* sp./*Paravilla* sp. was most common at Sidlee (77% of all visits) and at Triunfo (45%), while at Kirsten Lee the bee *Ashmeadiella californica* subsp. *californica* (78%) was more common (Fig. 1). A test of independence based on the eight most common visitor groups (*Ashmeadiella californica* subsp. *californica*, *Ceratina* sp., *Exoprosopa doris*, *Exomalopsis* sp., *Lepidanthrax* sp. and *Paravilla* sp., other Bombyliidae, Melyridae, and Syrphidae) showed there were significant differences in insect composition among sites ( $G^2 = 216.665$ ,  $df = 8$ ,  $P < 0.001$ ). Since the plants at the three sites bloom in a somewhat sequential order (Sidlee, Kirsten Lee, Triunfo) differences in insect composition were also analyzed for seasonal variation. A shift in dominance from *Lepidanthrax* sp./*Paravilla* sp. to *A. californica californica* to a combination of both is seen when insect composition is grouped by two-week intervals (Fig. 2). With little overlap in blooming time among sites, it is hard to distinguish whether location or season was affecting insect composition.

Flower-head density seemed to have relatively little effect on the composition of visitors. The accumulation of visits at increasing densities was plotted for the eight most

common types of visitors at the three study sites in 2008 (Fig. 3). In general, most of these curves are similarly concave, and only rarely did the relative importance of different insect groups change with density. One exception occurred at Kirsten Lee when *A. californica californica* increased in frequency at the highest densities and surpassed *Lepidanthrax* sp./*Paravilla* sp. bee-flies. *Ashmeadiella californica* subsp. *californica* might be viewed as a volatile pollinator, since it was abundant at Triunfo, abundant when flower densities were high at Kirsten Lee, and absent from Sidlee. The bee-flies were more consistently present in high frequencies.

In 2009, *A. californica californica* was the dominant insect visitor at two sites (48% of all visits at Kirsten Lee, 65% of all visits at Triunfo), and *Lepidanthrax* sp./*Paravilla* sp. was the second most frequent group at these sites (27% at Kirsten Lee, 19% at Triunfo; Fig. 1). Cumulative curves seemed similar to those seen in 2008 (Fig. 4), with minor exceptions. In 2009 at Sidlee, melyrid beetles and *Ceratina* bees were abundant visitors to flowers of potted plants placed outside of a patch. The test of independence comparing the composition of the eight most common visitor classes among the three sites was again significant ( $G^2 = 1419$ ,  $df = 14$ ,  $P < 0.001$ ). In addition to insect composition varying by site, it also changed through the season, although in 2009 *A. californica californica* were more uniformly abundant throughout the season than they had been in 2008. Most of the heterogeneity in 2009 came from insect community composition being different at the start of the flowering season when compared to the latter part of the flowering season.

In summary, *P. lyonii* attracted a variety of non-specialist insect visitors, but the abundant bees and bee-flies appeared to be the most important visitors. The details of

which animals were abundant varied, but in general *P. lyonii* flower heads usually received many visits by various insects that appeared to contact sexual organs and to carry pollen.

### Visitation in 2008

In 2008 there were 135 15-minute visitor censuses. The analysis of the visitation data was broken into the following parts.

(1) The Spearman's rank correlation showed a significant positive relationship between density and visitation ( $r_s = 0.259$ ,  $df = 133$ ,  $P < 0.005$ ). Quadrats with more flower heads received more insect visits than those with fewer flower heads (Fig. 5A).

(2) A logistic regression was done using  $\log(\text{density})$  as the independent variable (Fig. 5B). It was found that less dense patches were less likely to be visited than more dense patches (deviance  $G^2 = 10.59$ ,  $df = 1$ ,  $P = 0.001$ ). Nonetheless, this effect was very weak (McFadden's rho squared = 0.057).

(3) A model II regression was run on log-log transformed data when there was at least 1 visit. This yielded a reduced major axis slope of 1.072. This slope, or coefficient of allometry, did not significantly differ from 1 ( $t = 0.624$ ,  $df = 72$ ,  $P = 0.535$ ). In other words, as density increased, number of visits increased only as a proportion, with no per-capita Allee effect (Fig. 5C).

After this set of results, a general linear model was used to look at the effect of temperature,  $\log(\text{density})$ , and site on  $\log(\text{visitation}+1)$ . Both temperature ( $P < 0.001$ ) and density ( $P < 0.001$ ) had significant positive effects on visitation while accounting for site ( $R^2 = 0.234$ ,  $P = 0.018$ ,  $n = 135$  visitor censuses).

## Seed Set in 2008

There was no significant difference in seed set between hand-augmented and open-pollinated flower heads (Fig. 6A; proportion seed set transformed by squaring, paired  $t = 0.603$ ,  $n = 52$  pairs,  $P = 0.549$ ). Given that hand-augmentation versus open-pollination yielded a  $P > 0.25$ , seed set in subsequent analyses was represented as the average of the fruiting heads in each patch.

The effects of various predictor variables on average squared seed set were analyzed using a general linear model with stepwise elimination (when  $P > 0.25$ ). First temperature was eliminated ( $P = 0.901$ ). Next the  $\log(\text{visits} + 1)$  was eliminated ( $P = 0.682$ ). Density also did not significantly contribute to predicting seed set, though it could not be eliminated ( $P = 0.100$ ). Including density in the model, seed set differed among sites ( $R^2 = 0.209$ ,  $P < 0.001$ ,  $5n = 78$ ). Kirsten Lee had the highest seed set, while Triunfo had the lowest (Fig. 6B).

Using a regression with only one predictor, seed set was not related to the number of visits per head ( $P = 0.510$ ). Treating visitation as categorical (i.e. considering whether or not the patch received a visit), again revealed no significant effect on seed set (two-sample  $t = 0.107$ ,  $df = 76$ ,  $P = 0.915$ ).

## Visitation in 2009

In 2009, 15-minute pollinator censuses were done back-to-back. There were 254 pairs of censuses. Visits were variable between the first and second censuses. The added variance component among groups of censuses was 80.5% for the number of visits.

Changing the dependent variable to per-capita visits per head, the added variance component among groups was 44.6%.

The predictors of visitation were subjected to six analyses.

(1) A test of independence showed a significant difference on whether a flower head was visited or not based on if it was inside or outside of a patch ( $G^2 = 157.835$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 7 lower inset). The percent of quadrats that were visited was higher inside a patch (69%) than outside a patch (16%), but of course more flower heads were under observation inside a patch than the lone head that was watched outside a patch.

(2) The scatter of per-capita visitation rates against distance did not suggest an Allee effect (Fig. 7 upper graph). Visitation outside a patch was highly variable but sometimes higher than inside of a patch. If anything, lone flower heads were visited more often than flower heads in patches.

(3) When potted plants were categorized as visited or not visited, single flower heads inside of a patch were significantly less likely to receive any visits than those outside of a patch ( $G^2 = 3.986$ ,  $df = 1$ ,  $P = 0.046$ ; Fig. 8 inset). The percent of potted plants visited inside a patch (10%) was lower than outside a patch (16%).

(4) Looking at only data points that received one or more visits, the flower heads outside a patch sometimes received more visits than those inside of a patch (Fig 8). Once again there was no evidence that isolated individuals suffered from an Allee effect.

(5) A logistic model was run to test for the effect of temperature, density of flower heads, and site on whether flowers in a quadrat were visited or not. A simplified model without site was only marginally significantly different from the full model (deviance  $G^2$

= 4.83,  $df = 2$ ,  $P = 0.089$ ). Both temperature and density were highly significant and had positive effects ( $P < 0.001$ ; in the simplified model, McFadden's rho-squared 0.213).

(6) Rather different results were obtained modeling the effect of these predictors on whether or not the focal head was visited (instead of whether or not any flower head was visited). Site was highly significant ( $G^2 = 22.216$ ,  $df = 2$ ,  $P < 0.001$ ), with Sidlee having 25.8% of potted plants visited, Kirsten Lee having 11.9% visited, and Triunfo having 5.6% visited. Neither temperature nor density of flower heads had a significant effect on the probability of a focal flower head being visited ( $P > 0.2$ ).

#### Seed Production in 2009

(1) Whether seeds developed or not was modeled as a function of density, number of visits to the potted plant, site, and temperature. In the first model, visits was non-significant and poolable ( $P = 0.670$ ). Next temperature was eliminated ( $P = 0.642$ ). Then the deviance was calculated between a model with site and density versus a model with only site, and it was not significant ( $G^2 = 4.304$ ,  $df = 2$ ,  $P = 0.116$ ). In neither of these models was density significant ( $0.1 > P > 0.05$ ).

(2) For those cases in which heads produced seeds, the number of seeds that they produced was subjected to general linear modeling. The first variable eliminated was density ( $P = 0.864$ ). The number of visits to the potted plant also had no significant effect on seed number ( $P = 0.453$ ). In the final model, site had no significant effect ( $P = 0.091$ ) and temperature had a very significant negative effect with few seeds developing at the highest temperatures ( $P = 0.003$ ).

(3) Treating distance as a categorical variable, i.e., pots inside a patch versus those outside a patch, there was no significant difference in whether or not these individuals set seed ( $P = 0.095$ ). There was no apparent effect of distance on the number of seeds matured (Fig. 9).

(4) The 37 potted plants from inside patches for which number of seeds was scored can be considered by themselves as a data set paralleling the 2008 data. Using these data, there was no significant relationship between seed number and density ( $R^2 = 0.023$ ,  $P = 0.372$ ; Fig. 10).

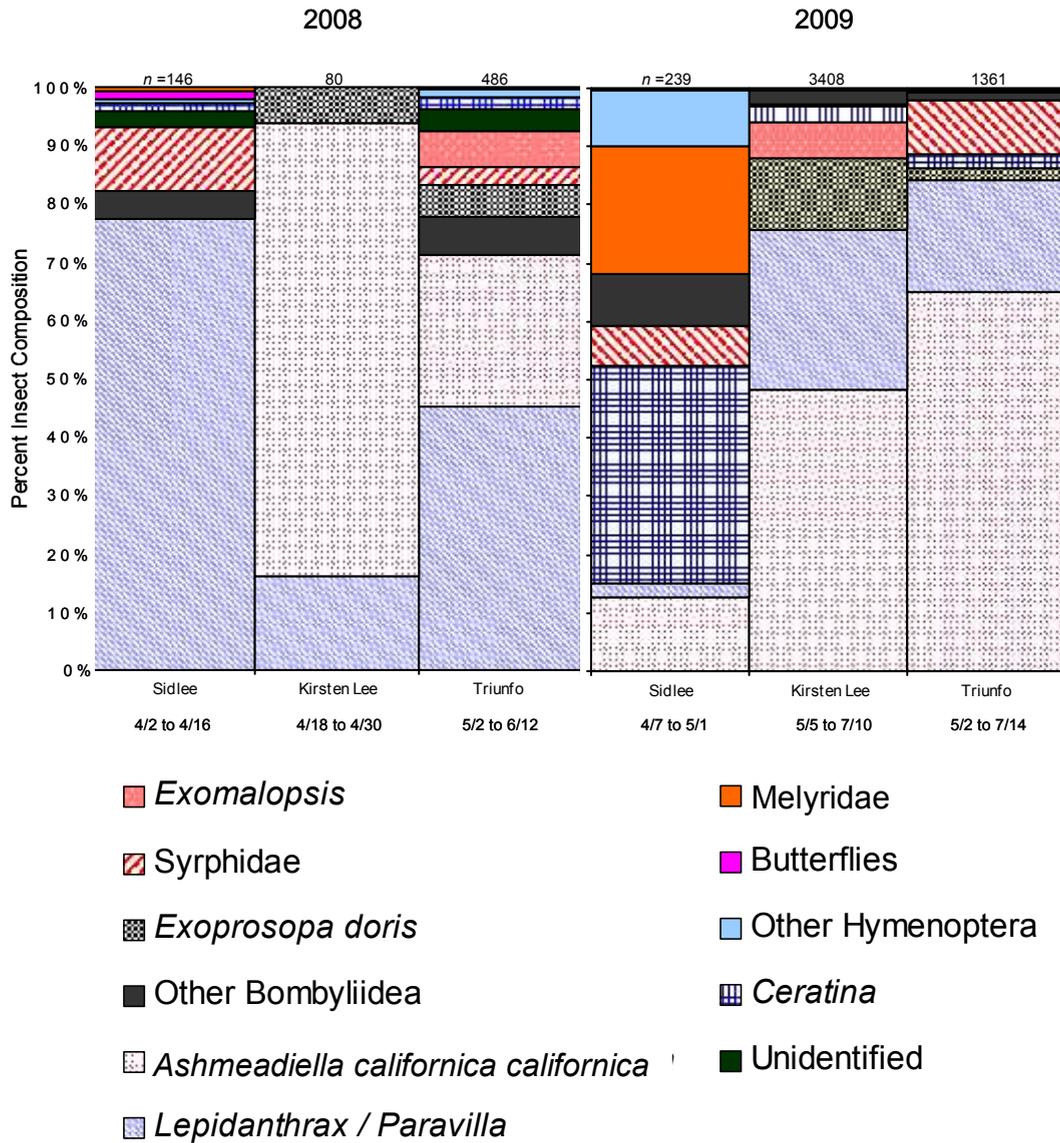


FIG. 1. Insect composition categorized by site. Although some sites appear to be dominated by one of the two common insect groups (*Lepidanthrax* sp./*Paravilla* sp. or *Ashmeadiella californica* subsp. *californica*), seasonal variation could be causing this pattern. There was also a difference in insect composition between years, where there were higher numbers of *Lepidanthrax* sp./*Paravilla* sp. in 2008 than 2009, and *Ashmeadiella californica* subsp. *californica* was more common across sites in 2009 than in 2008.

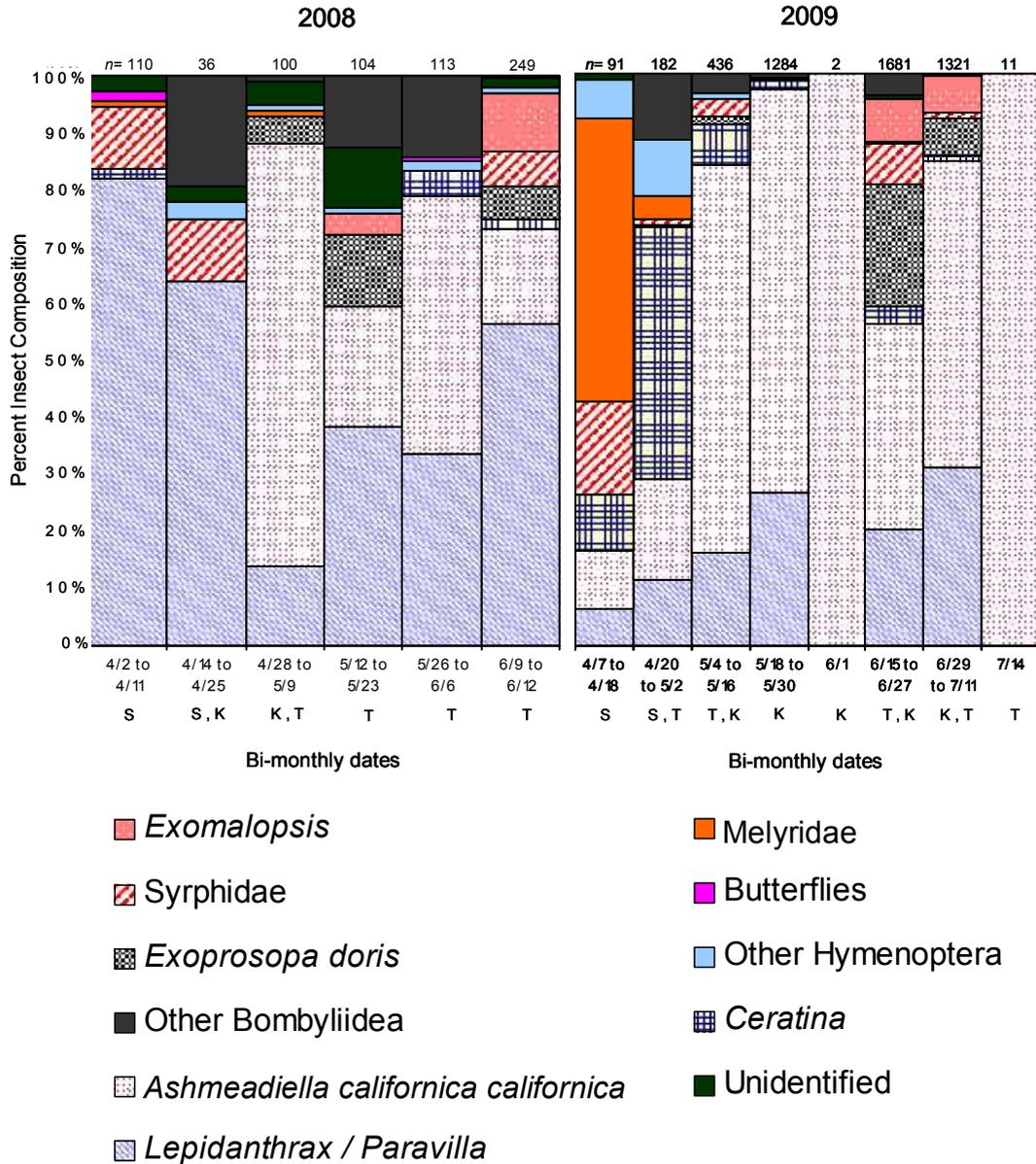


FIG. 2. Seasonal variation in insect composition broken into two-week intervals. The locations of the observations, listed below the dates, show that Sidlee was the first to bloom, while Triunfo was the last. Despite the variety in insect visitors, *Lepidanthrax* sp./*Paravilla* sp. or *Ashmeadiella californica* subsp. *californica* were generally the most common visitors.

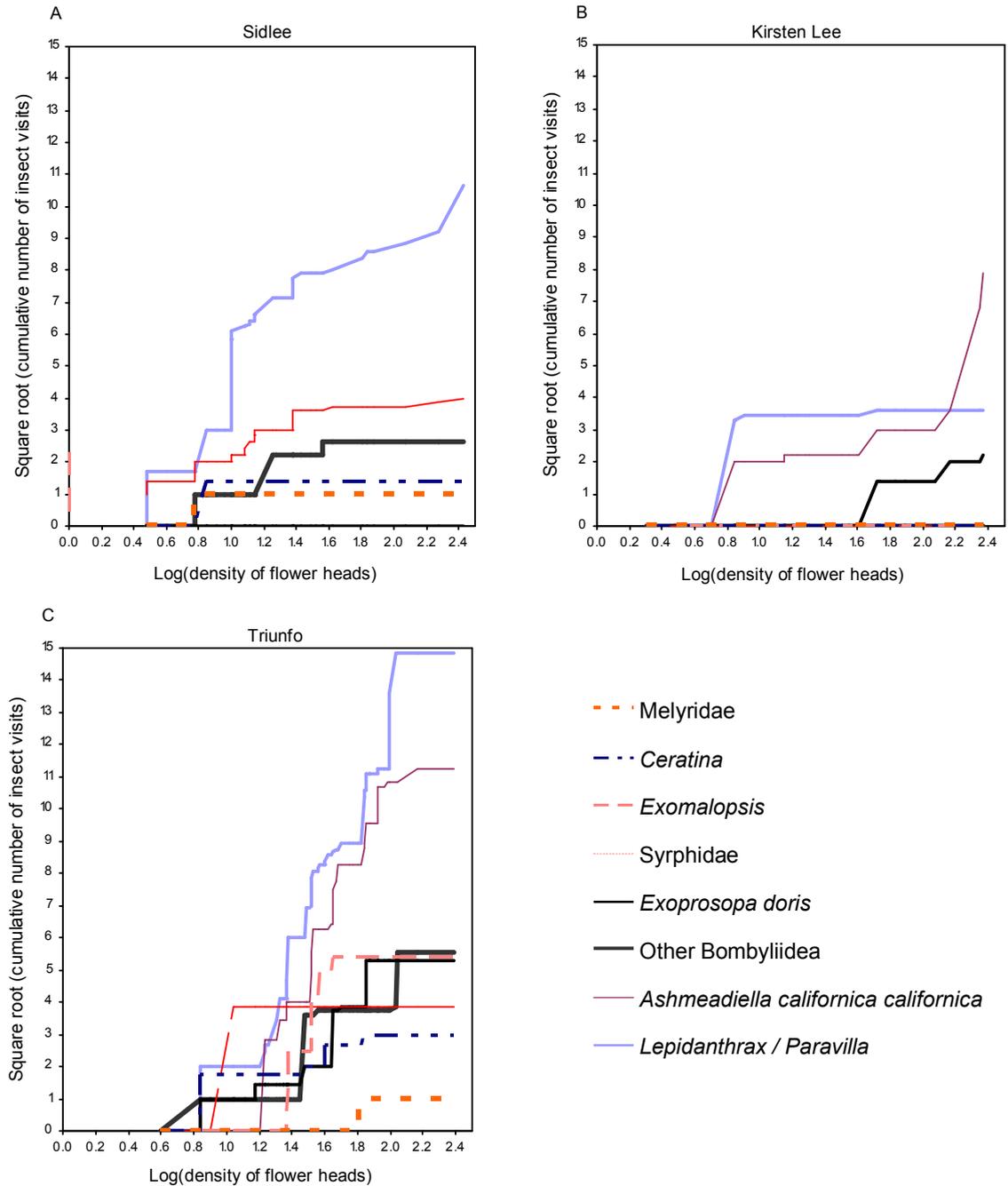


FIG. 3. Cumulative curves of visits in 2008 with increasing flower head density. Although less common insects show more leveling off with increases in density regardless of site, this could be an aberration of low abundance and not from a preference to visit low density patches. *Lepidanthrax* sp./*Paravilla* sp. were common across all sites and For common visitors, visitation increased after log densities of 0.8 (7 flower heads) with increases beyond log densities of 1.7 (50 flower heads) showing that some insects prefer higher density patches. (A) *Ashmeadiella californica* subsp. *californica* were not observed at Sidlee. (B) There were fewer insect groups observed at Kirsten Lee than at Sidlee or Triunfo. (C) The greatest accumulations of insects were at Triunfo.

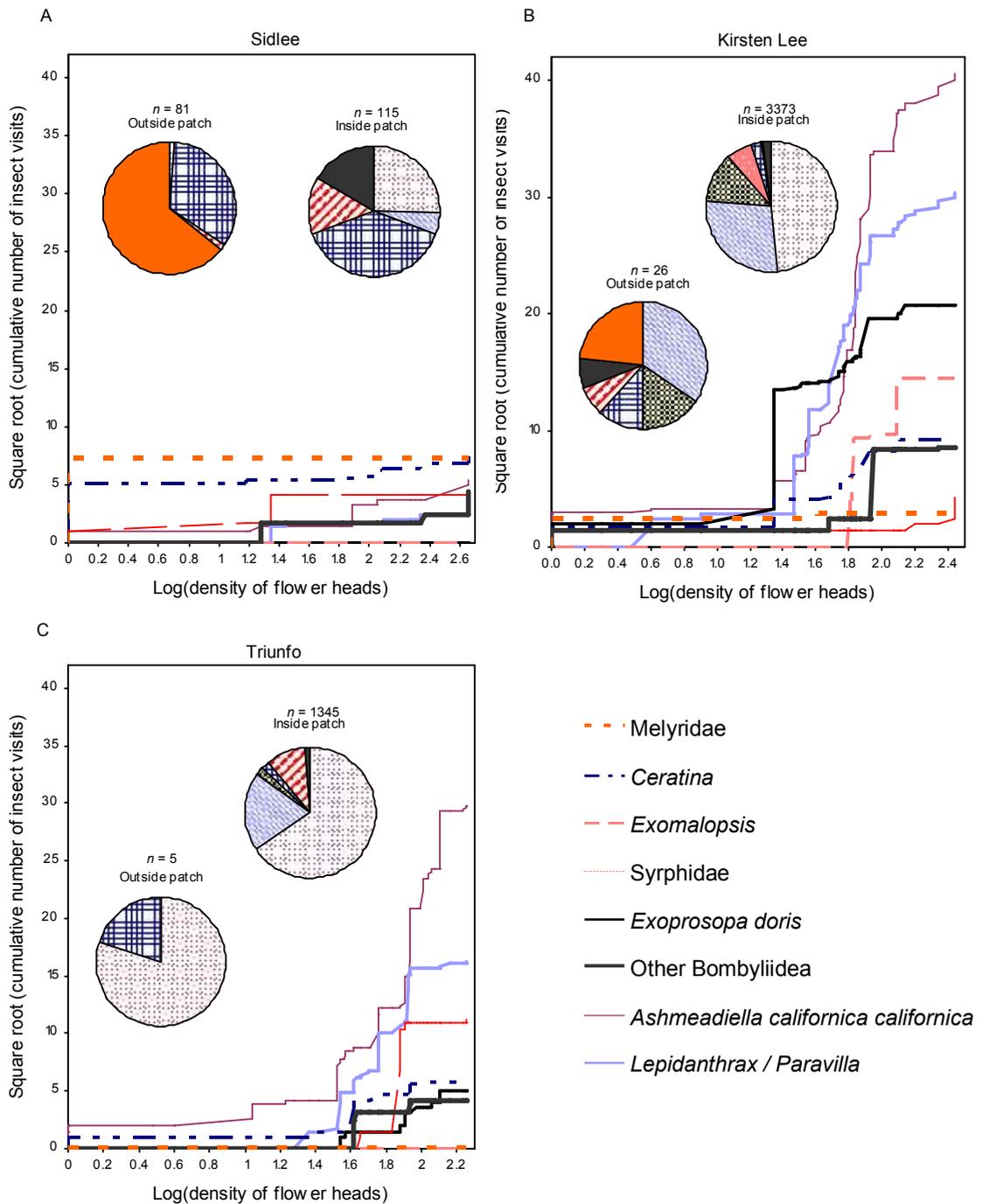


FIG. 4. In 2009, there were greater accumulations of visits in relation to density than in 2008. *Lepidanthrax* sp./*Paravilla* sp. and *Ashmeadiella californica* subsp. *californica* accumulated the greatest number of visits. Across all sites, insect visitation increased greatly after log densities of around 1.4 (25 flower heads). (A) At Sidlee, melyrid beetles were more common on flowers placed outside a patch. (B) *Ashmeadiella californica* subsp. *californica* were absent from flowers outside a patch at Kirsten Lee. (C) At Triunfo, *A. californica* subsp. *californica* was common to flower heads inside and outside a patch.

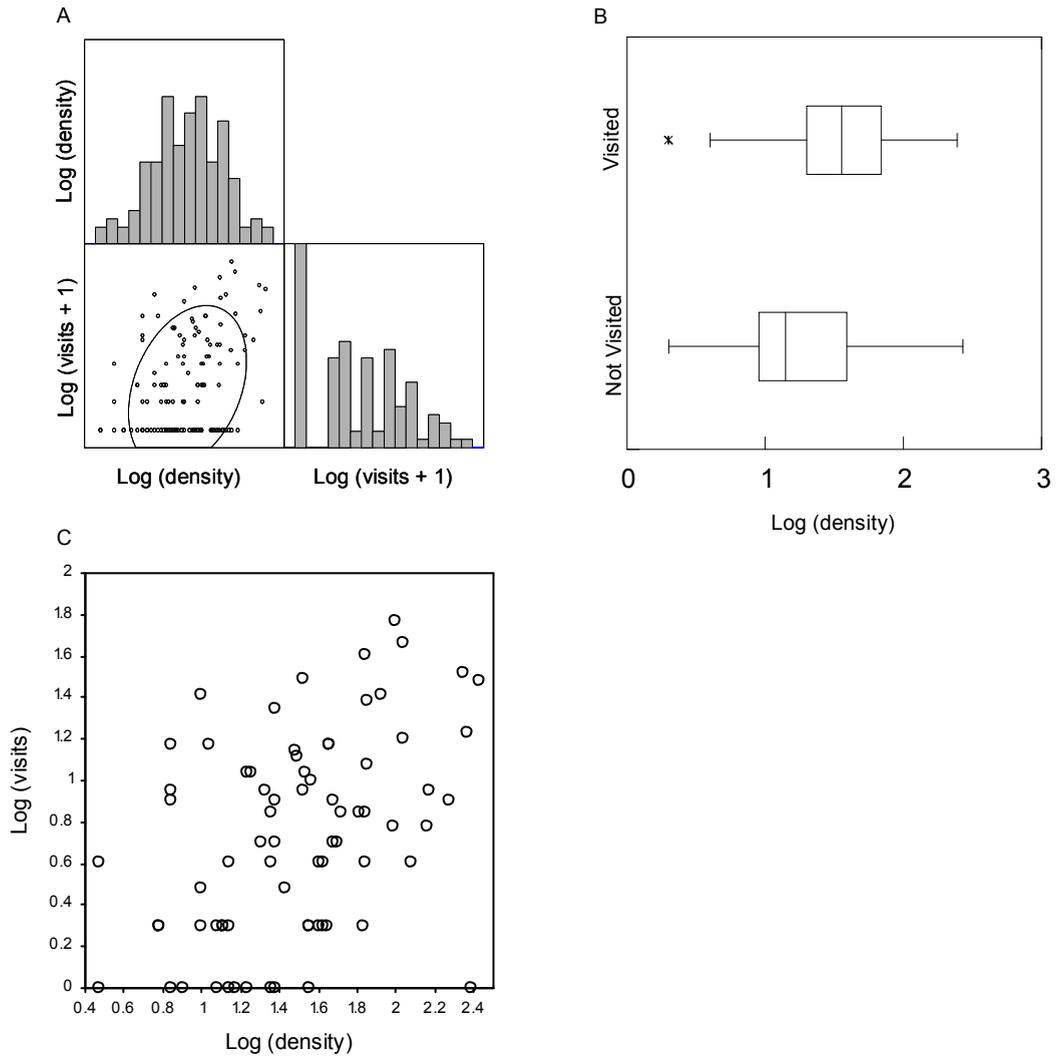


FIG. 5. Visitor censuses in 2008. (A) There was a correlation between  $\log(\text{visits} + 1)$  and  $\log(\text{density})$  represented by the ellipse  $r_s = 0.259$ ; note that zero visit observations were included. (B) Patches of varying densities differ in their ability to attract visitors ( $n = 135$ ). Patches of lower densities were less likely to be visited than more dense patches, although this relationship was weak. (C) For patches that received at least one visit, there was an isometric relationship between  $\log(\text{density})$  and  $\log(\text{visits} + 1)$ , not significantly different from 1 ( $P = 0.535$ ).

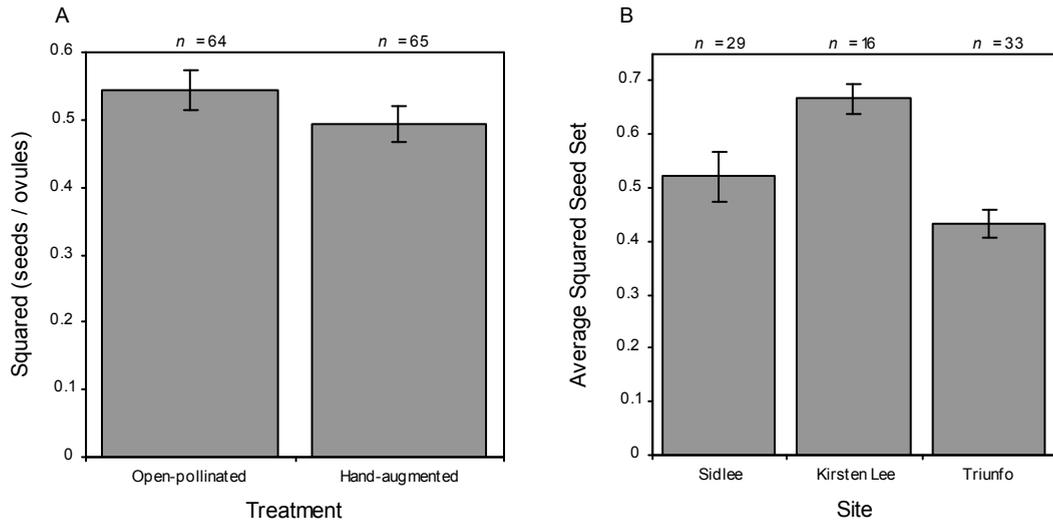
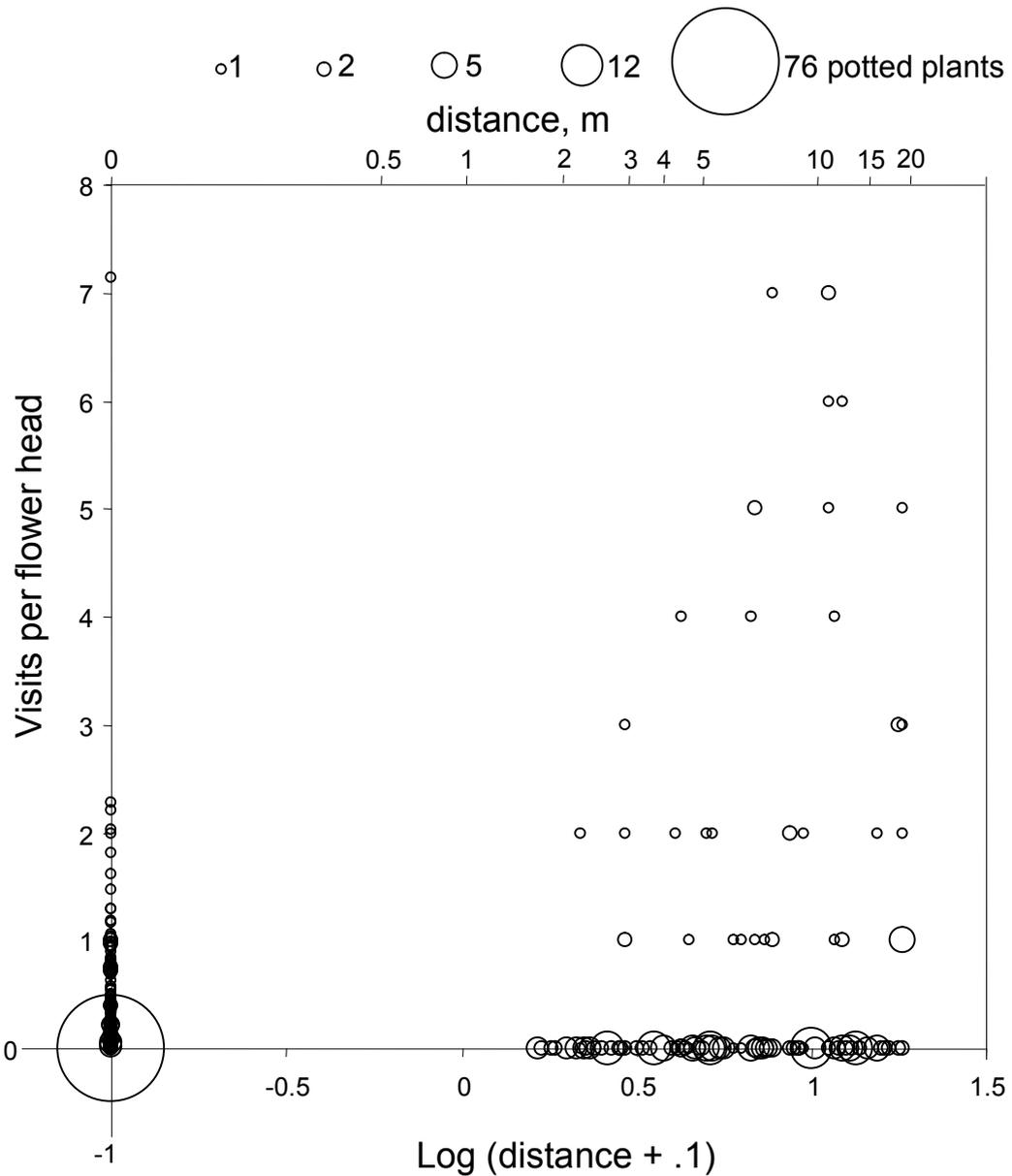
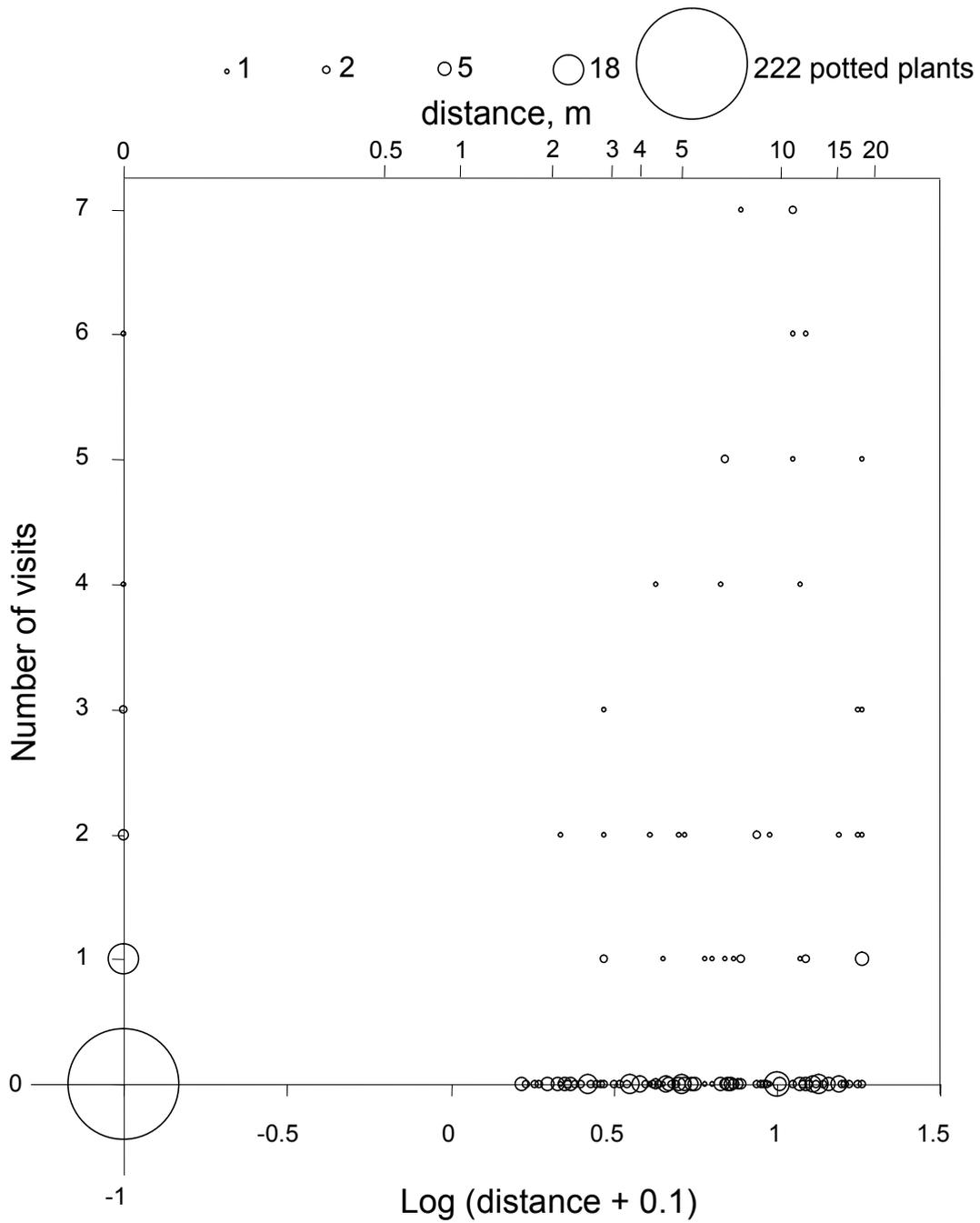


FIG. 6. Seed set data in 2008 and predictor variables. (A) Open-pollinated and hand-augmented flowers set about the same amount of seed, if anything hand-augmented flower heads had a slight decrease in seed set ( $n = 52$  pairs,  $P = 0.549$ ). This means that flower heads in chosen patches were not experiencing pollinator limitation. (B) Among variables site, density, temperature and visitation, site was the most important predictor of seed set. Kirsten Lee had the highest overall seed set, while Triunfo had the lowest (Sidlee  $0.521 \pm 0.047$ ; Kirsten Lee  $0.667 \pm 0.028$ ; Triunfo  $0.432 \pm 0.027$ ).



		Numbers of quadrats		
non-zero	171	46		$G^2 = 157.835$
zero	78	236		$df = 1$
				$P < 0.001$
	in a patch	outside patch		

FIG. 7. Visitation to flower heads in 2009. Lower left: Categorizing both visitation and location of a potted plant, there was a greater number of visits to the many flower heads inside of a quadrat than the one flower head outside a patch.



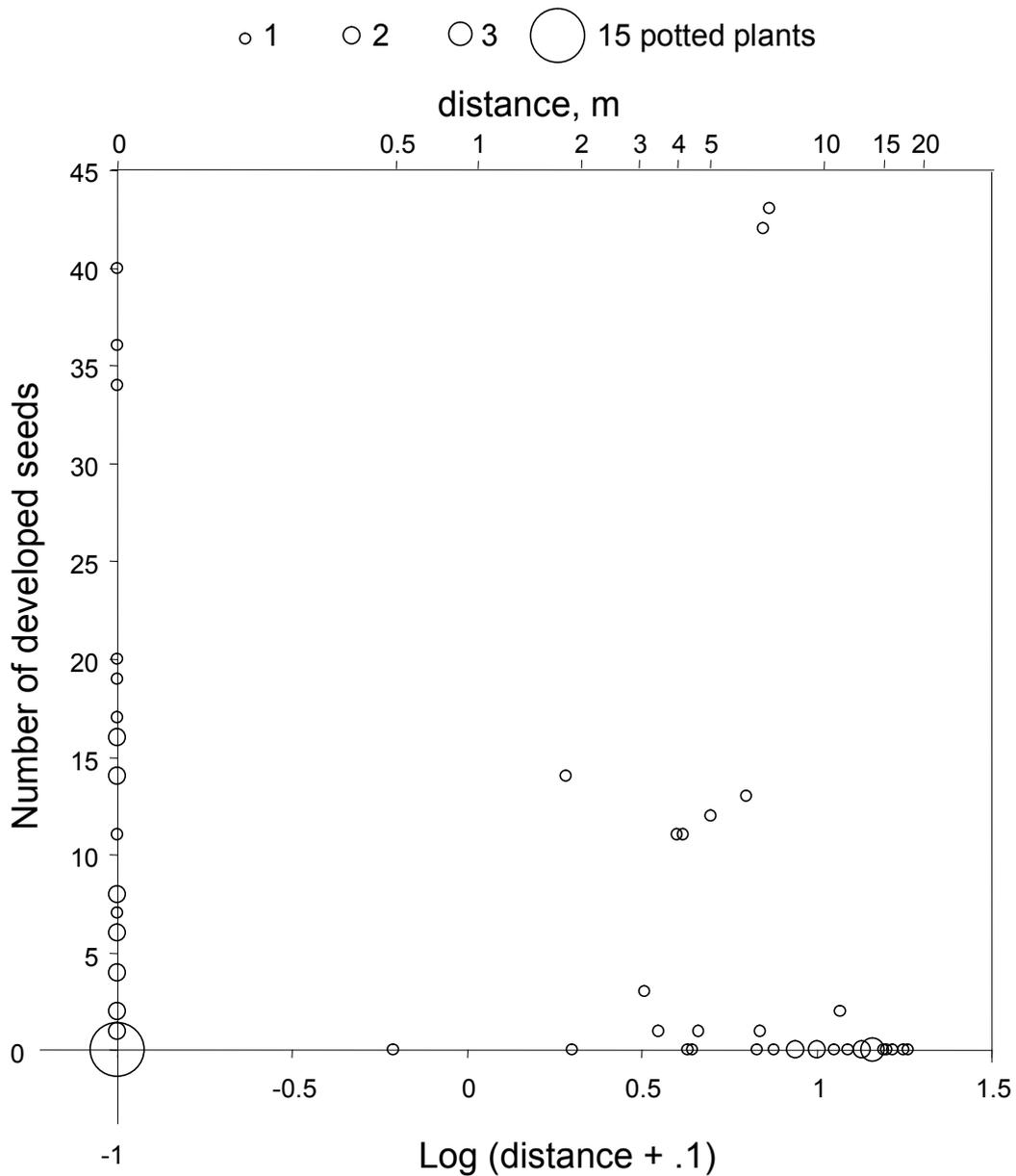
Numbers of potted plants

non-zero	25	43
zero	222	225

$G^2 = 3.986$   
 $df = 1$   
 $P = 0.046$

in a patch    outside patch

FIG. 8. Potted plant visits and distance in 2009. Lower left: individuals outside a patch were visited more.



Number of plants that set seed

non-zero	22	13
zero	16	21

$G^2 = 2.796$   
 $df = 1$   
 $P = 0.095$

in a   outside  
patch   patch

FIG. 9. Ovule development and distance in 2009. Log(distance + 1) did not influence the number of developed ovules. Lower left: Whether a flower head set any seed was not influenced by being inside or outside a patch.

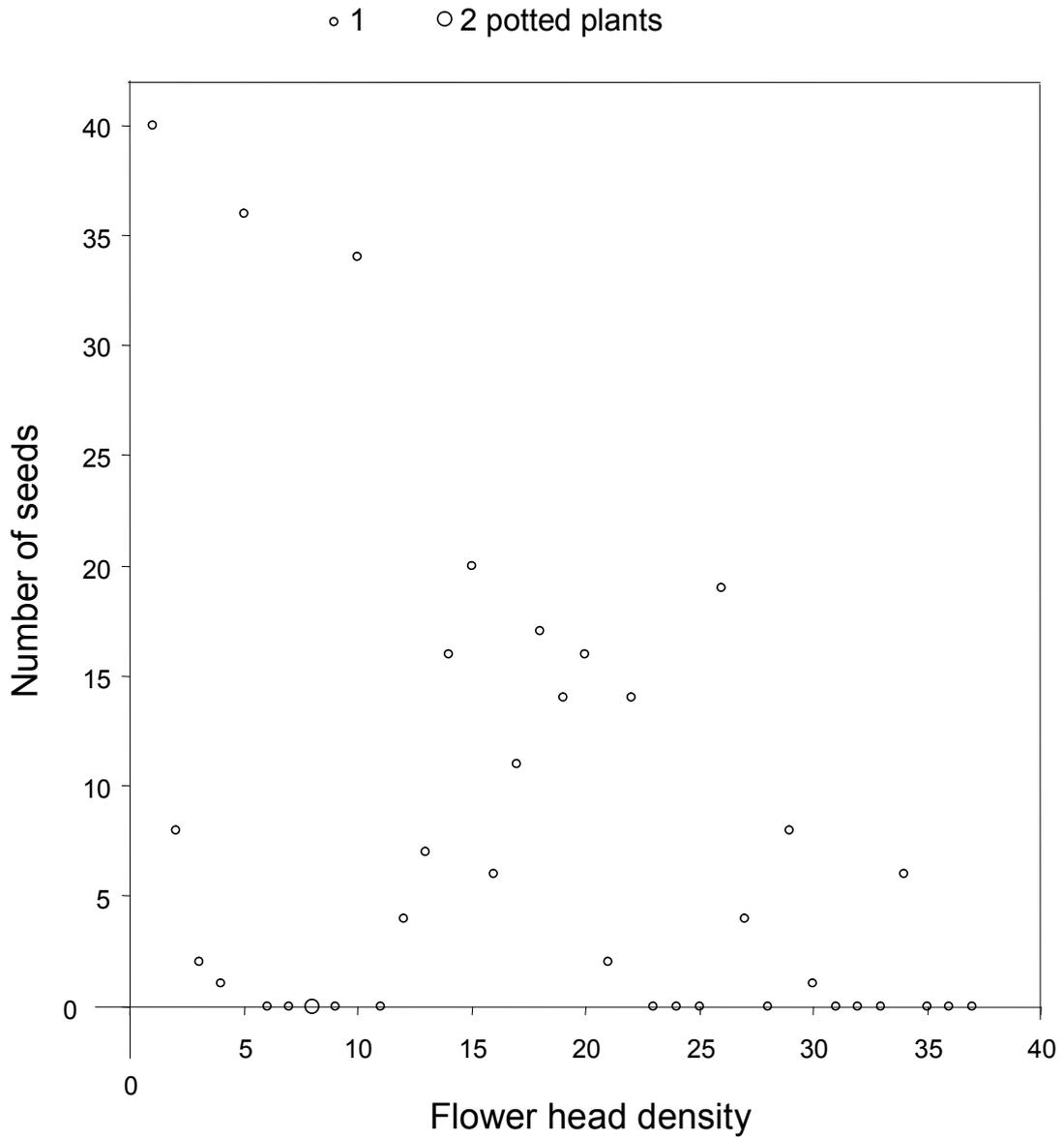


FIG. 10. Relationship of seed set and density in 2009, for the thirty-seven pots inside of a patch. There was no significant affect of density on seed development ( $P = 0.372$ ). The number of seeds a flower head produced varied with those in less dense patches sometimes producing more seeds than those in dense patches.

## DISCUSSION

### Interpretation

*Pentachaeta lyonii* does not seem to be experiencing strong component Allee effects. It may not be subject to them because of the variety of generalist insects that visit its flowers. In 2008, visitation in natural patches seemed to increase proportionally with density, and seed production was not related to density. In 2009, lone potted plants received at least as many visits as potted flower heads within a patch and sometimes more. Although the quality of visits to individuals outside of a patch could conceivably have been poor, the plants in pots placed some meters from a patch seemed to produce as many seeds as those inside a patch. These findings, however, did not address whether functioning pollination services at the individual level were contributing to overall population growth. Allee effects might still play a role at the demographic level and small populations might experience a different dynamic than the populations that were studied. However, the concern that poor pollinator services are exacerbating the decline of *P. lyonii* was not confirmed by these data.

*Pentachaeta lyonii* has a generalized pollination system using a diversity of bees and flies. Floral visitation records compiled by Hurd and Michener (1955), Hall and Evenhuis (1982), and Hall and Evenhuis (1984) show that these insects visit a wide variety of flowers in the coastal sage scrub community. The dominant insects alternated across sites and among the study years between the bee-flies *Lepidanthrax* sp. and *Paravilla* sp. and the bee *Ashmeadiella californica* subsp. *californica*. This switch in dominance was probably of little consequence since Braker and Verhoeven (1998) deemed both kinds of insect to be functionally adequate as pollinators. Although pollen

removal and deposition rates may differ from one kind of insect to the next, there may be functional saturation regarding seed development. In well-studied cases pollinator composition has been shown to vary by year or location (Herrera 1988; Bosch et al. 1997; Petanidou et al. 2008), and this variance may be of little consequence to a flower with generalist pollinators.

In the present study, variation in pollinator assemblage seemed to depend little on density in the surrounding square meter. It is possible that the insect's perception of what constitutes a foraging spot is greater than what was addressed here. Lone potted plants at Sidlee, however, were mainly visited by melyrid beetles and *Ceratina* bees in April. Of the eight dominant insect visitors to *P. lyonii* flowers, six showed irregular fluctuations rather than seasonal trends. Two kinds of insects that did seem to arrive late in the flowering season were the larger bee *Exomalopsis* sp. (mid May 2008, Mid June 2009) and the bee-fly *Exoprosopa doris* (late April 2008, mid June 2009). Even though both appeared late in the season, the difference in timing between years suggests a role for environmental factors such as precipitation or temperature.

The importance of insect visitation depends partly on whether a plant can self-pollinate. Keeley (1995) deemed *P. lyonii* to be self-incompatible. In an effort to double-check the determination of self-incompatibility, flower heads were enclosed in mesh bags (openings approximately 0.22 mm) and allowed to potentially self-pollinate (Appendix B). The results, however, were not consistent among flower heads. Out of 11 bagged flower heads, six had more than 10 percent seed development. *Pentachaeta lyonii* may have partial self-compatibility or the pollinator-exclusion bags may have failed to exclude tiny pollinators or exogenous pollen. Thrips are tiny potential pollinators that

were observed in corolla tubes of *P. lyonii*. Thrips have been shown to be effective pollinators in a variety of flowering plants (Moog et al. 2002; Mound 2005). To evaluate the role of thrips in the pollination of *P. lyonii*, an experiment involving plants with open-pollination and pollinator exclusions was attempted (Appendix B). Unfortunately, the results were inconclusive. The procedures of the experiment, such as the frequency of watering, spraying the plants with pyrethrin insecticide, or allowing bags to touch the plants, might have damaged flower heads. This line of study should eventually be reworked. Whether *P. lyonii* is partially self-compatible is not crucial information for interpreting the present results on visitation and seed production of flower heads exposed to natural pollinators. *Pentachaeta lyonii* needs pollinators for full seed set, and it is receiving enough pollinator visitation to avoid an Allee effect.

Plants in other studies have been shown to experience negative effects on seed production with decreases in density. Sih and Baltus (1987) reported that low densities of catnip (*Nepeta cataria*) had limited seed development. While Forsyth (2003) documented decreases in reproductive success for Haleakala silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*) individuals flowering asynchronously during low bloom years.

Unlike the aforementioned studies, Wagenius and Lyon (2010) found isolated *Echinacea angustifolia* (Asteraceae) received increased visitation when compared to plants in patches. This did not, however, result in increased pollen deposition or seed production. Large patches of the self-incompatible *Hymenoxys herbacea* (Asteraceae) had a similar dynamic of decreased visitation per head, but the overall increase in mate availability resulted in a tradeoff making pollen limitation negligible (Campbell and Husband 2007). In contrast, Elliott and Irwin (2009) found low density patches of

*Delphinium barbeyi* experienced increased seed production compared to higher density patches. This finding is similar to lone potted plants of *P. lyonii* producing equal or higher amounts of seed than plants in patches.

Perhaps the pollination of *P. lyonii* is facilitated by other co-occurring flowers. Sargent et al. (2011) found that *Lasthenia fremontii* occurring with other Asteraceae experienced less pollen limitation than individuals occurring with more distantly related, less similar plants. Often *P. lyonii* grows with *Lasthenia chrysostoma* and *Deinandra fasciculata*, with the beginning of *P. lyonii*'s blooming season overlapping the end of *L. chrysostoma*. This likely increases an insect's perception of flower density and facilitates the sharing of pollinators. A gradual presentation of pollen has also been shown to increase the quantity and the quality of pollination in *Keckiella* and *Penstemon* species (Thomson et al. 2000).

In addition to the potential benefit of co-occurring annuals facilitating pollination, *P. lyonii* growing with higher densities of native annuals may experience decreased competition with non-native grasses and forbs (Keeley and Swift 1995). It is reasonable to think that when factors such as gopher disturbance or resource reduction from non-native plants affects more common native annuals, this in turn negatively impacts *P. lyonii*. Thus thriving annual communities may mean reduced risks of *P. lyonii* patch extirpation.

Before the visitation data were collected, an appropriate amount of time for visitor censuses was determined. Researchers have successfully used a wide variety of times ranging from 10-minutes (Kirchner et al. 2005; Hansen and Totland 2006) to two 90-minute observations per experimental population (Kolb 2008). *Pentachaeta lyonii*

surveys roughly followed the 15-minute observations of Steffan-Dewenter and Tschardt (1999) and the 25-minute observations of Wolf et al. (1999). As a logistical matter, it seems unlikely that the data would have been improved by merely doubling the duration of the census. Back-to-back censuses suggested that 30-minute blocks of time would still yield data sets with zeros because whether a head was visited or not is apparently autocorrelated in time. To improve visitation as a statistical variable, one would need a number of short censuses throughout the whole period of stigma receptivity for focal plants in each patch. The sum of all visits across all censuses of a plant could then be used collectively as one data point. This would have made each data point better, but far fewer data points would have been gathered. For quantifying possible effects of density on visitation, more data points were deemed desirable. The 15-minute censuses allowed  $n = 135$  in 2008 and  $n = 515$  in 2009.

The experiment using potted plants examined the relationship between density and visitation better than the use of flower heads in natural patches. The use of potted plants allowed for a large sample size while minimizing variability. These results showed that visitation to an individual flower head was not lessened by being in a low-density patch or several meters outside a patch. The seed-set results were based on smaller sample sizes and on a 15- or 30-minute census, but they were still on a par with other studies (Kunin 1997; Parachnowitsch and Elle 2005). Furthermore, Groom's (1998) study on *C. concinna* subsp. *concinna* included *no* pollinator visitation data, simply relating increased seed production, positively, to the density of experimental patches.

Hand-augmenting pollen transfer did not increase seed production. It is reasonable to believe that there was no difference because open-pollination was plentiful,

but imaginable shortcomings of the experiment are worth mentioning. Perhaps not enough pollen was transferred via paintbrush, which might have been avoided by bagging pollen donors to obtain more pollen. Pollen may have been applied to open florets when not all stigmas were receptive. Another possibility is that stigmas were damaged from rough hand-augmentation. A control treatment consisting of brushing flower heads with a clean paintbrush could have tested for this possibility. In a review by Young and Young (1992), it was noted that 17 studies out of 99 reported a decrease in seed development with hand-augmentation. Some of the proposed explanations include pollen clogging, stigma damage during hand-pollination, the use of dead pollen, and missed stigma receptivity.

Although seed production did not differ between pollination treatments, it did vary by site. Site is a complex variable that inherently includes differences in the amount of sun cast onto the ground, flowering and fruiting season, and soil moisture during the time when seeds germinated and matured. Resource availability, rather than insufficient pollination services could have caused plants at Kirsten Lee to have greater seed production than individuals at Sidlee or Triunfo.

Temperature, measured at the time of the visitor census, can also affect plant reproductive success. In this study, high temperatures led to an increased number of insect visits, as insects are typically more active on warmer days. When considering whether seeds developed or not, temperature had no effect. However, among those flower heads that developed seeds, high temperature had a significantly negative effect in 2009. Although increased visitation rates were seen with increases in temperature, this likely had little effect on seed set since one or a few visits is all that is needed for seed

development. It is likely, for those plants that developed seeds late in the season when temperatures were high, that heat and associated dryness decreased stigma receptivity or led to ovule abortion. Such effects of physiological stress have been documented in other plants. Cross et al. (2003) found that heat decreased seed production and pollen viability in *Linum usitatissimum*. In a review by Zinn et al. (2010) increased temperature stress was noted to reduce stigma receptivity in *Prunus persica*, increase ovule abortion in *Arabidopsis*, and decrease pollen maturation in *Solanum lycopersicum*.

The generalized pollination system in *P. lyonii*, likely buffers it from negative Allee effects. Although dense quadrats received more visitation than less dense quadrats, this was not a per-capita increase. These results are unlike many other studies in which increased density has been found to have a positive effect on seed production and hand-pollination often results in increased seed production.

#### Conservation of *Pentachaeta lyonii*

Although the present study examined only pollination, other portions of *Pentachaeta lyonii*'s lifecycle should be reviewed to comprehend potential conservation approaches. This plant's dispersal ability is likely limited. Unlike the pappus on *Taraxacum officinale* that allows the achene to float in the air (Tackenberg et al. 2003; Green 2005), the pappus of *P. lyonii* easily breaks. Most seeds likely fall next to the parent plant, with little movement thereafter. This inability to disperse long distances may prevent new patches from becoming established. The meta-population dynamic may be more toward the loss of patches than the founding of new patches.

In the greenhouse, seeds readily germinate, and Keeley (1995) failed to find any seed dormancy whereby seeds could remain banked for years. Low bloom years followed by high bloom years suggest, however, that *P. lyonii* populations may contain seed banks (Population census records from the Santa Monica Mountains National Park Service, personal communication with Christy Brigham, and personal observation). Patches have also been noted to reappear after not being seen for years, such as at Stunt Ranch (sighted in 1990 and again in 2008) and on Santa Catalina Island (officially recorded in 1931 and again in 2011 at a different site), suggesting that *P. lyonii* has a seed bank dynamic. Tests for prolonged dormancy other than those done by Keeley would be worth doing and could include the measurement of germination success across moisture gradients. The potential lack or depletion of a seed bank in some populations, if indeed there is none, could contribute to the decline of *P. lyonii*; making the regular production of seed necessary for the maintenance of population size.

In an effort to increase the number of *P. lyonii* populations, Pucci (2006) seeded plots at Paramount Ranch, a location that did not contain naturally occurring *P. lyonii*. After the first season's bloom, the number of plants in those plots declined. There was limited success in establishing this new population. Associated with the current thesis and in an effort to determine suitable *P. lyonii* habitat, an unsuccessful population establishment experiment was attempted (Appendix B). Factors that may have contributed to recruitment failure included using seeds that were old, planting seeds too deep or too shallowly, choosing the wrong soil surface for sowing seeds, or most importantly planting seeds too late in the growing season. Morgan (1999) found the amount of precipitation *Rutidosia leptorrhynchoides* received was the most important

factor for population growth. Seedling death in *P. lyonii* could also result from inadequate moisture, granivory or competition with other plants. Moroney et al. (in press) showed that competition with non-native plants decreases both the size and number of inflorescences in *P. lyonii*, which presumably reduces seed production. These results are consistent with studies of California shrubs and grasses (D'Antonio and Mahall 1991; Dyer and Rice 1999, respectively). Negative effects of competition with non-native grasses have also been documented for other annual forbs (Kimball and Schiffman 2003; Corbin et al. 2007). In these studies non-native competitors decreased resources and soil moisture available to native plants resulting in decreases to native plant reproduction.

The Allee effect is not a main concern for conservation of *P. lyonii*. In 2008, individuals in low density quadrats still received sufficient visits to set approximately the same amount of seed as individuals in high density quadrats. Then in 2009, isolated flower heads were able to both attract insect visitors and set seed. This finding is important because it means that pollinator limitation is not what is preventing marginal expansion of *P. lyonii* populations. Unlike *Lasthenia chrysostoma*, which is ecologically general and has a wide distribution (Rajakaruna and Bohm 1999), *P. lyonii* is restricted to only a few populations likely because of its poor dispersal ability resulting in a narrow distribution. Poor dispersal coupled with poor competitive ability may deprive *P. lyonii* of a mechanism by which to avoid the more competitive non-native plants.

Although *P. lyonii* is a poor competitor with limited dispersal, the pollination portion of the lifecycle is functioning. Efforts to protect this California endemic should focus on habitat conservation, removal of invasive plants in small or low density populations, and new population establishment. Populations of *P. lyonii* that are now

extinct suffered from habitat alteration by non-native grasses or habitat destruction due to development. By finding a methodology for new population establishment, which would include soil analysis between currently inhabited sites and potential sites, continued survival of the species might be achieved.

Another important conservation factor is the accurate environmental assessment of areas being considered for development. Public awareness and the protection of natural open spaces play a role in the continued existence of *P. lyonii*. An important example was the battle for the Baldwin Westlake property, now known as Triunfo Creek Park. Although the Baldwin Company claimed they had first bid for the property, conservation-minded individuals at the Municipal Water district and Santa Monica Mountains Conservancy enlisted the help of a reputable environmental consultant. Carl Wishner documented the occurrence of a population of *P. lyonii* along with the presence of the rare *Dudleya cymosa* subsp. *agourensis* (Envicom Corporation 1992). After these discoveries, the Municipal Water District purchased the land from the FDIC and sold part of it to the Conservancy. This preserved over 400 acres of natural habitat and likely increased the values of the existing homes in the area as well as the outdoor experience available to residents.

The city of Thousand Oaks prides itself for having over 14,800 acres of open space. Nevertheless, populations of *P. lyonii* and other endemic plants continue to be threatened by development. Open spaces provide services that include hiking trails, native insects that pollinate both urban gardens (Frankie et al. 2002; Thorp et al. 2002) and agricultural plants (Kremen et al. 2002), and an outdoor lab with which to explore interactions between organisms. By planting gardens with a diversity of flowering native

and ornamental plants and refraining from the use of pesticides, urban areas can have high native pollinator diversity (Frankie et al. 2002). Residents have a voice in preserving natural habitat and can contact local or state representatives with their concerns. What an individual or community does to preserve natural habitat will determine not only the fate of those organisms but the ecosystem services left to posterity.

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APPENDIX A:  
POPULATION SURVEY METHODS

Patches within a population are surveyed using transect lines and  $0.5 \times 0.2$  m quadrats (Daubenmire quadrats). The method roughly follows those of Elzinga et al. (1998). Numbers one through 10 should be placed inside a hat and randomly drawn. Alternatively the number in the ones position on a digital watch can be chosen. The number drawn is used for the baseline transect. This baseline transect runs the whole length of a patch, from sparse outlying individuals through the patch itself. If the number seven is drawn, then a perpendicular transect would be placed at 7, 17, and 27 m etc. along the baseline transect. If the number 10 is drawn, the perpendicular line would be placed at 10, 20, and 30 m etc. along the baseline transect.

After the perpendicular transect is placed across the width of all visible *P. lyonii* in the patch a second number is drawn, by either method above. If the number five is drawn, the short side of the Daubenmire quadrat would start on 0.5, 1.5, 2.5, 3.5 m etc. for the length of the perpendicular transect. If nine is drawn instead, the short side of the quadrat would be placed at 0.9, 1.9, 2.9, 3.9 m etc. along the perpendicular transect. All *P. lyonii* plants (as opposed to the more numerous flower heads) in this quadrat would be counted. The Daubenmire quadrats should alternate sides along the perpendicular transect. If one were to face outward towards the end of the perpendicular transect and begin on the right hand side, the second quadrat would be placed on the left hand side and the next quadrat would return to the right hand side. In other words even numbers in the ones place (0.1, 2.1, 4.1) would have quadrats on the right side of the transect and odd

numbers in the ones place (1.2, 3.2, 5.2) would have quadrats on the left side of the transect. The total length of the perpendicular transect where *P. lyonii* occurs is recorded. In the instance where Daubenmire quadrats were placed on the nines (0.9, 1.9, 2.9, 3.9 m etc.), visible *P. lyonii* extended to 3.4 m, and counts are done up to 2.9 m, the total length of the perpendicular transect would be recorded as 3.4 m.

Once all perpendicular transects are surveyed, the total length of the baseline transect is recorded. The baseline transect extends to the last visible individual, regardless of whether this falls into the area surveyed by the perpendicular transect. If the baseline transect extends to 35 m, but the last perpendicular transect ended at 30 m (surveys on 10s: 10, 20, 30 m), the total length of the baseline would be 35 m.

The number of individuals in each perpendicular transect is estimated from the total number of plants in quadrats and the number of quadrats surveyed. First the average number of plants per m<sup>2</sup> is calculated as:  $10 \times \frac{\text{total \# plants}}{\text{total \# surveyed quadrats}}$ , where 10 is the conversion factor for the Daubenmire quadrat. Next the average number of plants per m<sup>2</sup> is used to calculate the total number of plants along the perpendicular transects.

$\text{Total Length} \times 10 \times \frac{\text{average \# plants}}{\text{m}^2} \equiv \text{total \# plants}$ . The total number of plants along each perpendicular transect is summed for each patch and the number of individuals per patch (baseline transect) is summed for all patches to estimate the total population size.

APPENDIX B:  
OTHER STUDIES ATTEMPTED

A test of self-compatibility was done on individuals from the Sidlee site. Eleven flower heads that had not yet bloomed were selected haphazardly from different plants. Then the flower heads and part of the stem were placed in mesh bags. Bags were tied at the bottom and affixed to a wooden stick to support the fragile stem. After seeds had time to develop, heads were collected and seeds were counted.

Six out of eleven bagged heads produced seed. Of those six that produced seed, the percent seeds produced were 1.47, 3.23, 9.09, 31.25, 73.33, and 84.0. The higher percentages suggest either a potential ability to self or a failure of the bags to keep out all pollinators. Thrips are small enough to fit through the holes in the mesh bags and were seen on some flower heads. It is unknown whether thrips have the potential to contribute to pollination of *Pentachaeta lyonii*.

During visitor observations in 2008 thrips were observed pushing pollen around inside *P. lyonii* florets. Thrips are cosmopolitan and have been largely ignored for their role in pollination (Mound and Terry 2001; Mound 2005). Although some thrips are pollen parasites, they carry a few pollen grains on their bodies and their abundance can make them effective pollinators (Momose et al. 1998; Yi-Bo and Zhen-Yu 1999; Mound and Terry 2001; Williams et al. 2001; Mound 2005).

The pollination efficiency of thrips was studied in 2009 using potted plants. Potted plant treatments included open-pollination, pots enclosed in fine mesh (<0.2 mm openings) that was not accessible to thrips, or pots enclosed in mesh accessible to thrips

but not other insects. Plants were first treated with a pyrethrin based insecticide to eliminate the presence of thrips and other insects. Next the plants were haphazardly selected for one of the treatments. Plants placed in bags received a long wooden stick to minimize the top of the bag resting on the plant. The opening at the top of the bag was sealed with double sided duct tape. The top of the bag was pushed firmly together and sealed on the exterior with more duct tape.

When flower heads began to senesce the bag was removed from the plant and dry flower heads were collected. Flower heads that were still green were individually re-bagged for later collection.

Thrips were observed in florets of all treatments, even the thrips exclusion treatment. Neither plants exposed to open-pollination nor thrips treatments, however, produced mature ovules. The lack of seed development in the open pollination treatment suggests that the experimental design was flawed. Perhaps the plants were too large to have sufficient resources for seed production and should have been trimmed. The experiment may have been done too late in the season to allow open-pollination treatments a sufficient number of visitors and interspecific pollen. Spraying plants with the oil based pyrethrin may have interfered with stomatal conductance and trials without pesticide application may have been more successful. Further studies should be done to re-test the thrips hypothesis using smaller plants earlier in the season.

U.S. Fish and Wildlife (1999) stated that attempts to mitigate habitat loss by sowing seeds and planting seedlings have failed. With increasing habitat alteration and destruction, it is important to determine how to establish new viable populations. New population establishment was attempted at Paramount Ranch, a previous site of

population establishment experiments. Different substrates of varying percent cover were selected. Seeds were planted late in February after the majority of winter rains. Seeds from each of the three study sites were used (Sidlee, Kirsten Lee, and Triunfo), with 12 seeds from each site per plot. Each 1 × 1 m plot contained three plots of 36 mixed seeds. There were a total of 28 quadrats for a total of 3,024 seeds. The seeds did not germinate in 2009, possibly due to planting after most of the winter rain. In 2010, plots were surveyed, but no *P. lyonii* were seen. In 2011, only eight individuals were observed in one of the plots. The lack of seedling establishment could have been from insufficient moisture due to planting after the majority of winter rains, planting seeds too deep in the soil, from seeds or seedlings being eaten, or some combination of the aforementioned conditions.

In the future, studies examining new population establishment should perform soil and mycorrhizae analysis on prospective plots and plots where *P. lyonii* currently grow. Seeds should also be planted in November or December, before winter rains begin. Suggested variables for measurement include relative water content of soil, percent cover of plants 1 m around each plot, and soil compaction.