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A TEST OF DENSITY-DEPENDENT POLLINATION WITHIN THREE POPULATIONS OF ENDANGERED *PENTACHAETA LYONII*

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Abstract—A major concern with endangered plants is that they might attract insufficient numbers of pollinators, produce low numbers of seeds, and decline towards extinction. We examined effects of density as it varied within populations on the pollination of *Pentachaeta lyonii*, an endangered species that requires pollinators for seed set. Generalist bee-flies and bees were abundant pollinators at three sites for two years. Per-capita visitation rates did not decline at sparse points or for plants placed on the order of 10 m away from other flowering individuals. Seed production was not pollinator-limited within patches, but seed set was low beyond 10 m from neighbours. Considering prior findings, factors such as habitat loss, competition with alien plants, and poor establishment of new populations likely contribute to the rarity of *P. lyonii* more than pollination failure.

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

INTRODUCTION

A major conservation concern surrounds the possibility that organisms at unnaturally low densities might reproduce poorly causing their populations to decline towards extinction (Courchamp et al. 1999, 2008). The kind of density-dependence in which sparse populations fail is called “inverse density dependence”; it is a positive relationship between density and success. In contrast, “negative density dependence” is when vital rates dampen at high densities. Considering both kinds of density dependence, patches of flowers at both low density and at high density ought to, in theory, receive insufficient numbers of pollen grains to fully set seed, whereas patches of flowers at medium density ought to receive the most visits per capita (Rathcke 1983). The question then becomes, for any particular endangered species, are densities too low, overwhelming, or at adequate medium levels?

Many researchers have studied pollination success among populations of different sizes (Groom 1998, 2001; Steven et al. 2003; Field et al. 2005; Feldman 2006). In contrast, we are concerned with density as it varies within a population and within the field of view of a pollinator (Kunin 1997a,b; Dauber et al. 2010). As pollinators decide where they will forage, they assess not just individual blossoms but aggregates of flowers (Sih & Baltus 1987). Flowers at low-density points may be unable to attract visitors and fail to set seed. Plants growing some distance from the main population may likewise fail to reproduce. The population may be unable to grow outwardly at its margins for lack of pollination (or for other reasons).

Pentachaeta lyonii A. Gray (Asteraceae) is an endangered species. The U.S. Fish and Wildlife Service (1999) specifically suggested that reduced pollinator visitation might contribute to its decline. The species is self-incompatible and dependent on generalist pollinators (Fotheringham & Keeley 1998). One visit by either a bee or a bee-fly is about equally effective at causing a flowering head to set seed (Braker & Verhoeven 2000, 2002). The concern is that *P. lyonii* populations, after having declined for other reasons, have entered into a downward cycle in which sparse and/or small populations attract few pollinators and set few seeds (Moroney et al. 2011). Here we tested for declines in visitation rate and in seed production at decreasing point densities as surveyed throughout three natural populations of *P. lyonii*. In 2008 wild plants were studied as they occurred at varying densities throughout the populations. In 2009 we placed plants in pots throughout the populations to measure pollination success.

MATERIALS AND METHODS

Pentachaeta lyonii (Fig. 1) is an annual sunflower that occurs in openings in coastal sage scrub, a vegetation type that is shrinking due to suburban development (Davis et al. 1994; Minnich & Dezzani 1998; Rundel 2007) and due to type-conversion into alien annual prairie (D’Antonio & Vitousek 1992; Keeley 2004). We studied three populations, all near Thousand Oaks, California: EO24 (0325061, 3787047 UTM), EO11 (0329184, 3778060 UTM), and EO27 (0332072, 3778067 UTM). Each population was composed of patches that varied in area and density, ranging from plants isolated from others by distances on the order of 10 m up to a few hundred flowering heads per m^2.

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FIGURE 1. *Pentachaeta lyonii.*

Visitation in 2008

In 2008 from March to June, we quantified insect visitation as it related to flowering density. On any given day, we positioned a number of 1 × 1 m quadrats so as to study a range of densities, and we scored density as the number of open flower heads of *P. lyonii* in a quadrat. Quadrats in the three natural populations contained from 2 to 270 heads. The number of visits was counted as the number of times an insect landed on a head and contacted disk florets during a 15-minute census. Censuses were done between 10:00 a.m. and 4:30 p.m. We accumulated $n = 135$ censuses in 135 quadrats.

Seed Set in 2008

In each quadrat, we tested for pollen limitation of seed set. After the visitor census, two flowering heads were chosen to be similar in size and blooming stage. Each was marked with a numbered tag. One was randomly assigned to be hand-supplemented; the other was open-pollinated. We used a paintbrush to pick up pollen from flowers in the surrounding area and to transfer it to the supplemented head. Approximately two days later, when the ray petals of a tagged head began to wither, we covered the plant with a mesh bag supported by a wooden stake. After the pappus began to protrude from the bracts, about a week later, we collected the fruiting head. We counted the number of developed seeds and the number of undeveloped ovules (either not fertilized or aborted). We were able to evaluate seed set for $n = 52$ pairs of hand-supplemented and open-pollinated heads. For 24 additional cases one head of a pair could be scored.

Visitation in 2009

In 2009, we performed a phytometer study. Phytometer studies use plants to measure the quality of the environment at each of many points (Clements & Goldsmith 1924; Wilson 1995; Kniskern & Rausher 2006). In our case, each phytometer was a plant in a pot trimmed to present one flower head. When a plant had a head that was about to open, it was trimmed of any other open heads. Phytometers were placed so that the surrounding densities of natural *P. lyonii* varied. Phytometers were left in place to develop until the head was fully open, which took 1 to 3 days. Then, density was measured in one of two ways. (1) For phytometers with no other *P. lyonii* within a surrounding 1 × 1 m quadrat, the average distance to the three nearest blooming *P. lyonii* plants was measured. (2) For phytometers placed such that other *P. lyonii* shared a 1 × 1 m quadrat, density was measured as the number of open heads in the quadrat surrounding the phytometer and including it. The latter measure gives a more discerning index of density when it is seen at the scale of meters. The former measure prevents ties when no other flower heads are within the quadrat. We combined these two measures into a variable that we call "rank density." The phytometer with the lowest rank density was the one with the greatest average distance to its neighbours. The phytometer with the highest rank density was the one that had the most neighbours in its quadrat. This rank ordering of density nearly eliminates ties. We had 129 phytometers positioned outside of quadrats ($n = 36$ from 18.2 m down to 10 m distant from naturally occurring *P. lyonii*; $n = 40$ from 10 m down to 5 m distant from other *P. lyonii*; $n = 53$ from 5 m down to 0.56 m distant from other *P. lyonii*). We had 119 phytometers located inside of quadrats (which varied from having 2 to 455 open heads). Visitor censuses were done from April to July in the three study populations. We censused visitors for 30 minutes per phytometer (i.e. two 15-minute visitor censuses, usually back to back).

Seed Production in 2009

Phytometers were left in place until the corollas began to wither. Then the head was bagged until seeds had time to set, which took 1 to 2 weeks. Mature seeds were counted as in 2008, but undeveloped ovaries were not counted because maturing heads were collected at a less uniform stage than in 2008. Without the number of undeveloped ovules, seed production in 2009 was merely the number of mature seeds without a denominator.

Data Analysis

Three analyses were performed on the 2008 visitation data. First, a Spearman's rank correlation related visitation to number of flower heads in a quadrat, i.e., to density. Second, a logistic regression used log(density) as the predictor variable and whether or not a quadrat was visited as the response variable. Associated with logistic regression, McFadden's ρ^2 quantified the strength of the relationship. Third, for those quadrats that received at least one 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, i.e., accelerating or decelerating.

The 2008 seed-set data were squared to improve normality of residuals, so the dependent variable was $[\text{seeds/florets}]^2$. Squaring is a simple instance of a power transformation (Sokal & Rohlf 1995). It resulted in residuals that were more normally distributed than the more commonly used arcsine-square root transformation. For numbers greater than zero, squaring is a monotonic transformation. Some analyses were based on differences, i.e., [seed set in the hand-supplemented head]^2 – [seed set in the open-pollinated head]^2. We transformed before subtraction because subtracting is equivalent to including a random blocking variable in the analysis, and the variates before subtraction are therefore more fundamental (Sokal & Rohlf 1995). The differences were also approximately normally distributed. We started with an analysis of covariance in which the dependent variable was the difference between the squared seed set values and the independent variables were log(density) and population. Next, we used a paired *t*-test comparing hand-supplemented flower heads to open-pollination heads. Pairing focused the analysis on testing for an effect of supplemental hand pollination, blocking out variation among quadrats and populations. Average squared seed set was also analysed. We used a general linear model with three predictor variables: log(visits + 1), density, and population. This model was simplified after log(visits + 1) yielded $P > 0.25$ (the threshold for dropping terms recommended by Quinn & Keough 2002).

For our 2009 visitation analyses, we report only on visits to phytometers. A generalized linear model with a Poisson error structure was used to relate the number of visits during 30 minutes to rank density, simultaneously accounting for which of the three populations the phytometer was placed in. The use of ranks is very similar to the use of non-parametric statistics (Conover & Iman 1981). Ranks are robust protection against uneven distributions, and when ties are few, the use of ranks is nearly as powerful as a parametric test (Quinn & Keough 2002). We transformed only the independent variable and only in analyses for which we are primarily testing the null hypothesis of no relationship (not trying to parameterize a function for data that tightly follow a curve).

For 2009 seed production, 70 fruiting heads from phytometers were scorable. Number of seeds produced was plotted against rank density. A generalized linear model with a Poisson error structure was used, also accounting for the three populations.

Significance testing was performed in SYSTAT 11, except for the generalized linear models involving Poisson distributions, which were performed in SPSS 20.

RESULTS

Over the course of two years, we observed 5,720 insect visits while watching 24,012 flower heads during 15-minute visitor censuses. In other words, the number of visits per head was 0.238, which extrapolates to 7.6 visits per 8 mid-day hours during which any given stigma would have been receptive. The common visitors, in order of abundance, belonged to the families Bombyliidae, Megachilidae, Apidae, Syrphidae, and Melyridae. Particularly common were bee-flies (in the genera *Lepidanthrax*, *Paravilla*, *Exoprosopa*) and bees (in the genera *Ashmeadiella*, *Ceratina*, *Exomalopsis*). All these animals carried pollen and contacted stigmas. They are generalist foragers that visit many other kinds of flowers.

Visitation in 2008

Number of flower heads in a quadrat significantly and positively predicted number of visits to those flower heads; this correlation included zero-visit censuses ($r_s = 0.259$, $n = 135$, $P < 0.005$). The logistic regression showed that less dense patches were less likely to be visited than more dense patches (deviance $G^2 = 10.59$, $df = 1$, $P = 0.001$), but this effect was very weak (McFadden's $\rho^2 = 0.057$). The model II regression yielded a reduced major axis slope of 1.072, a number that 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 of number of heads, with no per-capita increase in visitation rate associated with increasing densities.

Seed Set in 2008

The average number of florets in a head was 50, and the average seed set was 72%. In the analysis of covariance of the differences between supplemented and open-pollinated heads, log(density) had no significant effect ($P = 0.348$; Fig. 2), nor did population ($P = 0.401$). In the paired *t*-test, seed set did not differ significantly between hand-supplemented and open-pollinated heads (respectively 70% versus 74% back-transformed from mean of squared proportions 0.493, SE = 0.0259, $n = 65$ versus 0.544, SE = 0.0291, $n = 64$; paired $t = 0.603$, $n = 52$ pairs, $P = 0.549$). In the analysis of average squared seed set, log(visits +1) was not a significant predictor and was dropped ($P = 0.682$). In the simplified model, density did not significantly contribute to predicting seed set ($P = 0.100$); that model accounted for differences among the three populations ($P < 0.001$).

Visitation in 2009

Phytometers measured whether there was a change in pollination success from points 18.2 m from neighbours to quadrats with hundreds of other flowering heads (Fig. 3). We found negative density dependence, i.e., the denser the

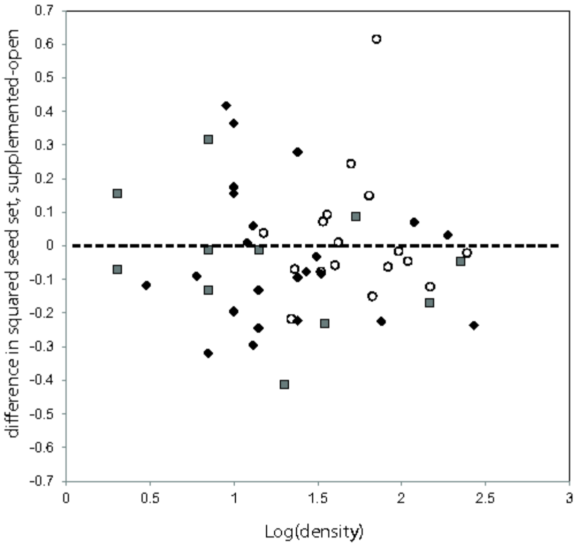

FIGURE 2. Pollen-limitation not found and not dependent on density. The three symbols denote the three study populations (diamonds=EO24; squares=EO11; circles=EO27). The dashed line indicates the null hypothesis for the paired *t*-test.

point, the fewer the visits to the phytometer (Wald χ^2 = 8.68, *df* = 1, *n* = 256, *P* = 0.003); the three populations also varied significantly in visitation rate (Wald χ^2 = 58.89, *df* = 2, *P* < 0.001).

Seed Production in 2009

Only 27% of the phytometers used to measure visitation were undamaged and available to be scored for seed production, and only 6 seeds per head were produced on average. Contrary to the visitation results, no seeds were produced on the phytometers that were placed farthest from neighbours, whereas seeds were more often produced on phytometers that had been placed amid other flowering *P. lyonii* (Fig. 4). Inverse density dependence was detected (Wald χ^2 = 125.16, *df* = 1, *n* = 70, *P* < 0.001), with the three populations also varying significantly (Wald χ^2 = 116.35, *df* = 2, *P* < 0.001).

DISCUSSION

The populations of *P. lyonii* that we studied received plenty of pollinator visits. Flowers were generally visited repeatedly over the course of a day. The visitors belonged to various species of insects that seem to be effective pollinators and that are generalist floral foragers (Holt 2011). In 2008 visitation increased in proportion to density. In 2009 isolated phytometers received more visits than phytometers placed within a patch.

Consistent with the visitation data, seed set in 2008 was not pollen limited and was not related to density. However, in 2009 the ten most distant phytometers failed to set seed, a finding that is at odds with our other results. One possible explanation is that visitors to the most isolated phytometers may not have been carrying pollen. Unfortunately, our data on seed production in 2009 are weak. The phytometers were water stressed after pollination, and they had to be handled several times. Many phytometers had to be eliminated from the analysis because their fruiting heads were damaged. Thus, the apparent inverse density dependence in seed production in 2009 could be an artifact, or it could be due to the distance the farthest phytometers were from other flowering *P. lyonii*. In theory, there is some distance that is too far for pollinators to be both attracted and carrying conspecific pollen.

Our study relates to topics that are often discussed as the Allee effect, which is when small or sparse populations collapse. A distinction is sometimes made between a "demographic Allee effect"—a decrease in average fitness in small populations—versus a "component Allee effect"—a decrease in individual fitness with decreasing density (Stephens et al. 1999). Not all failures to mate at the individual level translate into decreases in population growth (Ashman et al. 2004; Price et al. 2008), and not all demographic Allee effects among populations can be detected by merely studying variation within populations (Gascoigne et al. 2009). Our results indicate that poor visitation was not causing declines within the sparse areas of the three large populations that we studied. Poor pollination is unlikely to be the reason *P. lyonii* does not fill in the

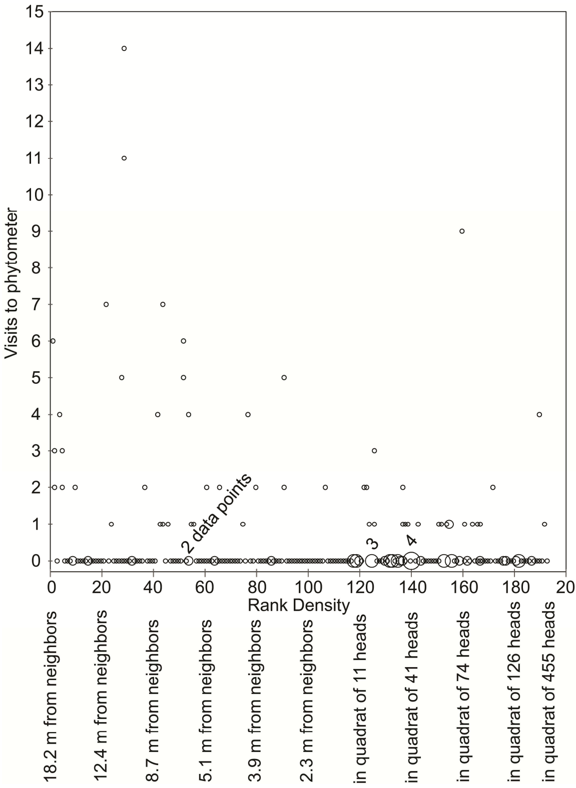

FIGURE 3. Phytometer visits in 2009 scattered against rank density. Bubble size indicates the number of overlapping data points. Density had a negative effect on visitation.

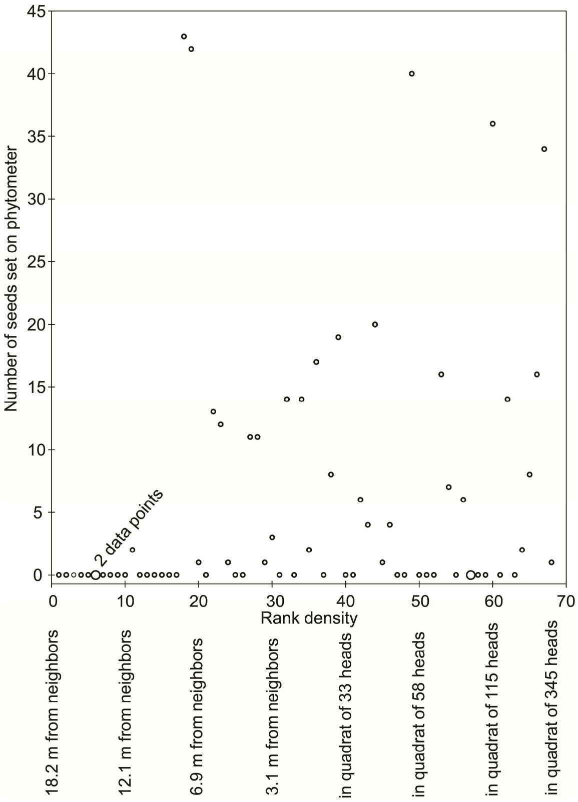

FIGURE 4. Seed production in 2009 scattered against rank density. Bubble size indicates number of overlapping data points. Phytometers placed the farthest from other flowering *P. lyonii* produced zero seeds.

sparse areas between patches and expand outwardly from the margin. Nevertheless, we did not study truly isolated, small populations, which might suffer from a low rate of pollinator visitation.

Experiments with other plants have found considerable pollination of plants isolated by greater distances than we studied. For *Dianella revoluta* R. Br., conspecific pollen deposition declined from 0 to 50 m from a pollen source; however, at greater spatial scales pollen deposition, if anything, increased as arrays were placed 1 to 5 km away from a nature reserve (Duncan et al. 2004). For *Delphinium nuttallianum* Pritz., arrays of 16 emasculated plants isolated by 50 to 400 m received less pollen than control plants in natural patches, but pollen receipt was still far from zero (Schulke & Waser 2001). Given such findings, it is not surprising that we found that pollinators visit flowers only meters from dense patches.

The potential for pollination to depend on density has been studied in other systems, often with results more alarming than ours. In *Senecio integrifolius* (L.) Clairv., a species that has declined due to changes in land use, decreased density was found to reduce reproduction (Widén 1993). In the narrow endemic *Banksia goodii* R. Br., plants in small populations were found to reproduce less than plants in larger populations, and the smallest populations produced no fertile cones at all (Lamont et al. 1993). In *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* Meyrat, a taxon in which most plants flower together in high-bloom years, plants that flowered during low-bloom years had decreases reproductive success (Forsyth 2003).

Low density does not necessarily lead to poor pollinator visitation. Isolated plants of *Echinacea angustifolia* DC. have been shown to be visited more than plants in patches, although that increase did not result in increased seed production (Wagenius & Lyon 2010). Such results mirror our phytometer results with *P. lyonii*. A similar dynamic was found for *Hymenoxys herbacea* (Greene) Cronquist—small patches received increased visitation per flowering head, but because of a decrease in mate availability, pollen limitation was only negligibly density dependent (Campbell & Husband 2007). In our study, the window of intermediate densities within which flowers were well pollinated ranged from plants isolated by about 10 m up to densities of much more than 100 plants per m^2.

To comprehend the limits on population growth of any endangered species, one should consider each segment of the lifecycle (Caughley 1994; Holt 2011). (1) *Pentachaeta lyonii* might suffer from poor seed dispersal with new patches rarely becoming established even in suitable habitat. Dispersal might amount to little more than seeds dropping on the ground next to the parent plant. (2) Seed germination might be problematic. Seeds remain viable for years in the lab, but they might germinate too readily in nature, not waiting until a year when the weather promises to allow *P. lyonii* to do well (Keeley 1995). Seed banks might end up being depleted by years in which many seeds germinate but few plants mature. (3) The growth of plants and the number of flowers produced is negatively impacted by competition from alien plants (Moroney et al. 2011). Extant populations of *P. lyonii* live in compact inorganic soils, often in places where competitors are sparse, yet when raised in pots and given ample water, plants can grow many times larger than individuals found in the field. These various clues suggest that competition is restricting the populations to isolated areas where the soil is too harsh for alien dominance. (4) Since the pollination portion of the lifecycle is working well, efforts to protect *P. lyonii* should address other stages.

An obvious first-priority for conservation is preventing destruction of any more populations of *P. lyonii*. Adding new populations should also be considered. The metapopulation dynamics of *P. lyonii* have been more toward the loss of populations than the establishment of new populations. A method should be developed for multiplying seeds in a nursery and then starting new populations in nature from seed. Pucci (2006) attempted to plant one new population from seed. After the first season's bloom, the number of plants at that site declined. Future researchers should use a multiple-regression approach to find factors that will predict successful establishment of new populations.

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