Floral display size, conspecific density and florivory affect fruit set in natural populations of \textit{Phlox hirsuta}, an endangered species

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INTRODUCTION

Population decline and extinction are determined in part by the abundance and density of individuals (Goodman, 1987; Dennis, 1989; Menges, 1992). In addition to experiencing environmental and demographic stochasticity (Lande \textit{et al.}, 2003), individuals in small, low-density populations often have reduced fitness due to mate limitation (Kramer \textit{et al.}, 2009). The positive relationship between population size (or density) and individual fitness (i.e. Allee effect, \textit{Allee et al.}, 1949) is commonly observed in plants (Lamont \textit{et al.}, 1993; Groom, 1998; Forsyth, 2003; Davis \textit{et al.}, 2004; Steven and Waller, 2007) and is particularly strong in self-incompatible species with few S-alleles (Levin \textit{et al.}, 2009; Young and Pickup, 2010). Failed fruit set in self-incompatible species can be due to the absence of compatible pollen grains on stigmas (Wilcock and Neiland, 2002; Aizen and Harden, 2007) and/or the presence of self pollen grains on stigmas (Galen \textit{et al.}, 1989; Waser and Price, 1991; Ramsey and Vaughton, 2000; Ruane \textit{et al.}, 2013). Thus, factors that affect the frequencies of self (incompatible) versus outcross (compatible) pollinations may ultimately determine patterns of fruit and seed set in self-incompatible species.

The number of flowers open simultaneously on a plant can affect both the number and the composition of pollen grains deposited on stigmas. Although larger floral displays attract more pollinators (Klinkhamer and de Jong, 1990; Miyake and Sakai, 2005), they also increase geitonogamous self pollination by encouraging pollinators to transfer pollen between different flowers within the same plant (de Jong \textit{et al.}, 1992; Barrett \textit{et al.}, 1994; Harder and Barrett, 1995, 1996). In self-incompatible species, geitonogamous self pollination can reduce fitness, as self pollen grains are capable of clogging stigmas, interfering with outcross pollen germination or tube growth, and/or usurping ovules (Ockendon and Currah, 1977; Waser and Price, 1991; Sage \textit{et al.}, 2006). The detrimental effects of self pollination on female fitness are often most pronounced when self pollen grains reach stigmas before outcross pollen grains (Broyles and Wyatt, 1993; Scribailo and Barrett, 1994; Ruane \textit{et al.}, 2013). Thus, natural variation in fruit and seed set may be explained by factors that determine the frequencies of self and outcross pollinations.

The frequency of outcross pollination can be influenced by the density of conspecific plants that are flowering nearby. Plants in high-density areas attract more pollinators, receive more outcross pollen grains, and generally have higher fitness than plants in low-density areas (\textit{Allee et al.}, 1949; Feinsinger \textit{et al.}, 1986, 1991; Klinkhamer and de Jong, 1990; Knight, 2003). High conspecific densities may also increase fitness by decreasing the frequency of geitonogamous self pollination, as pollinators are less likely to transport pollen between flowers on the same plant when many conspecifics are flowering nearby (Pyke \textit{et al.}, 1977; Pyke, 1978). Consequently, plants...
with large floral displays may be less prone to geitonogamous self pollination and its associated fitness costs when growing in high-density areas. Outcross pollination between nearby individuals is only expected to increase fitness if individuals are surrounded by genetically compatible neighbours and if individuals do not compete with each other for resources and/or pollinators (Rathcke, 1983; Fritz and Nilsson, 1994; Baker et al., 2000).

Fruit and seed set can also be affected by a variety of other factors, including petal colour, pollinator effectiveness, florivory and pre-dispersal seed predation. Petal colour can influence fitness via its direct effects on pollinator foraging patterns (Waser and Price, 1981, 1983) and/or its pleiotropic effects on the ability of plants to tolerate stress (Bazzaz et al., 1982; Turelli et al., 2001; Irwin et al., 2003). Variation in fitness can also be due to the abundance of effective pollinators (Mayfield et al., 2001; Moeller, 2005) or to the presence of herbivores that eat flowers (Irwin et al., 2004; McCall and Irwin, 2006) or unripe fruits (Hainsworth et al., 1984; Östergård and Ehrlén, 2005; Ågren et al., 2008). Florivores decrease fitness by destroying reproductive parts of the flower and/or by discouraging pollinator visitation (Krupnick et al., 1999; Pohl et al., 2006; Cardel and Koptur, 2010). Similarly, animals that consume undeveloped seeds within unripe fruits can dramatically reduce fitness, ultimately affecting plant abundance and distribution (Louda, 1989; Brown and Heske, 1990; Hulme, 1998; Howe and Brown, 2000, 2001).

Studies that quantify the underlying biological causes that affect the fitness of rare and endangered species can guide effective recovery efforts, assuming seed production limits population growth (Schemske et al., 1994). The objective of this study was to use non-destructive approaches to evaluate the reproductive ecology of Phlox hirsuta, a self-sterile endangered species. Specifically, we (1) quantified floral display size, local conspecific density, petal colour, florivorous beetle density and pre-dispersal seed predation within three populations and (2) determined whether these traits explained naturally occurring variation in fruit set. Although P. hirsuta is self-sterile, it is prone to self pollination and its associated fitness costs (Ruane et al., 2013). Thus, we expect fruit set to be highest in individuals that avoid self pollen interference by discouraging self pollination and/or by encouraging outcross pollination.

**MATERIALS AND METHODS**

**Study species and sites**

Phlox hirsuta (Polemoniaceae) is an endangered species endemic to serpentine soils in northern California (USFWS, 2000, 2006). P. hirsuta is a semi-woody perennial that grows in compact clumps. Individual plants reach 5–15 cm in height and produce flowers for approximately 7–10 weeks between early March and early June depending on the weather and elevation of the population (Ferguson et al., 2006). The total number of flowers each plant produces ranges from three to 818 (Ruane et al., 2013) and is positively correlated with plant size ($n = 374$, $R^2 = 0.44$, $P < 0.0001$). During peak flowering, an average of 64.5% ($n = 376$, s.e. = 1.3%) of an individual’s flowers are open simultaneously and insects are commonly observed moving between flowers on the same plant. Self pollen grains not only fail to sire seeds themselves, but also interfere with the ability of outcross pollen to sire seeds (Ruane et al., 2013).

Petal colour ranges from white (very rarely) to dark pink. Individual flowers remain open for approximately 8 d, fading to white during the last 2–3 d of anthesis (L. Ruane, pers. observation). Although species from ten orders have been observed visiting P. hirsuta flowers (Ruane et al., 2013). Diptera, Hymenoptera and Lepidoptera are the most frequent visitors (Ferguson et al., 2006). Following pollination, seed-containing fruits require 35–45 d to ripen in the field. Although each ovary contains three ovules, rarely does more than one seed per fruit develop; for example, 15, 83 and 2% of fruits resulting from natural pollinations in the field contained zero, one and two seeds, respectively ($n = 325$; L. Ruane, unpubl. res.). Thus, fruit set can be used to estimate total seed set in this species.

This study took place in three of the five known P. hirsuta populations near Yreka in Siskiyou County, California, between April and July 2013. The China Hill population (41°44’44”N, 122°36’55”W) contains thousands of plants scattered across approximately 19 ha of an open ridge and adjacent slopes; the Cracker Gulch population (41°40’08”N, 122°43’02”W) contains 1003 plants on 5.8 ha; and the Greenhorn population (41°43’04”N, 122°41’04”W) contains 1315–2065 plants over 8.1 ha. Greenhorn differs from the other two populations in that it comprises about nine discrete sub-occurrences, which probably resulted from habitat fragmentation due to human activities (USFWS, 2006).

**Data collection**

Before quantifying floral display size, local conspecific density, petal colour, florivorous beetle density, pre-dispersal seed predation and fruit set, we tagged a total of 376 plants (125–126 plants within each of three populations). Tagged plants spanned each population’s geographical range. During peak flowering, floral display size was estimated by counting the number of open flowers. A digital picture was taken above each plant (with a scale bar visible) so that plant size could be determined using ImageJ software (Schneider et al., 2012). Local conspecific density was estimated by recording the number of P. hirsuta individuals that were flowering within 1- and 2-m radii of each tagged plant. To quantify petal colour, we assigned a numerical value that ranged from 1 (completely white) to 12 (very dark pink) by comparing each plant’s petal colour with a gradient of colours on a paint chip (A5, Ace Hardware, Oak Brook, IL, USA). Petal colour could not be determined for 15 tagged plants on China Hill because a heavy rain removed their petals before colour was quantified.

The number of florivorous beetles on each plant was also recorded during peak flowering. Beetle density was calculated by dividing the number of beetles on each plant by the total number of reproductive structures (buds, open flowers, wilted flowers). If the total number of reproductive structures exceeded 25, then bamboo skewers were used to construct a grid on top of each plant to ensure accurate counts. To assess whether differences in beetle densities on a single day were indicative of more long-term differences, we recorded the number of beetles on each plant again 3–6 d later and we counted the number of damaged flowers on each plant. Flowers were recorded as damaged if they had bite marks, holes and/or missing petals.
accompanied by the presence of frass. The number of damaged flowers was divided by the total number of flowers for which florivory could be assessed to calculate the percentage of flowers damaged by beetles on each plant.

Approximately 4 weeks after peak flowering in each population, plants were revisited to quantify fruit set, which is a good indicator of total seed set in this species because the majority of enlarged ovaries contain a single seed. The number of enlarged and non-enlarged ovaries on each plant was counted to calculate percentage fruit set. In some cases (68 of the 376 plants), mammals (i.e. rabbit, hares and/or deer) consumed reproductive structures after peak flowering but before fruits were ripe. Severed stems were used as evidence of granivory by mammals. When plants experienced granivory, we used the total number of reproductive structures (counted during peak flowering) to calculate the percentage of reproductive structures eaten by mammals and percentage fruit set.

To identify the floral organs eaten by florivorous beetles, we examined 180 flowers (36 plants × 5 flowers per plant) that had one or more damaged petals on China Hill. After recording the number of petals eaten, flowers were dissected and the presence/absence of damage to stamens, stigmas and styles was recorded. Stamens were scored as damaged if a portion of an anther was missing. This is probably a conservative estimate of stamen damage, as beetles were seen inserting their heads within corolla tubes (probably eating pollen) without noticeably damaging anthers. Stigmas were scored as damaged if one, two or three of their stigma arms were missing. When all three stigma arms had been removed, style length was compared with other style lengths on the same plant to determine whether it had also been damaged.

Analyses

Wilcoxon tests were performed to determine how categorial variables (i.e. floral display size, total number of reproductive structures, number of fruits, number of plants within 1 m, number of plants between 1 and 2 m, and petal colour) differed among populations. Similarly, one-way analyses of variances (ANOVAs) were performed to determine how continuous variables (i.e. plant size, beetle density, percentage of flowers damaged, percentage of unripe fruits eaten and percentage fruit set) differed among populations. To determine if differences between population means were statistically significant ($P < 0.05$), Wilcoxon each pair and Tukey’s HSD tests were performed for categorical and continuous variables, respectively. Simple regressions were used to determine if larger plants produced larger floral displays, more reproductive structures and more fruits.

Simple regressions were also used to determine whether the number of beetles on each plant during peak flowering correlated with the percentage of flowers damaged on that plant and to determine if the density of beetles on each plant remained constant over time. Logistic regressions were used to determine whether the presence/absence of stamen, stigma or style damage depended on the number of petals eaten. Stigmas, styles and anthers are positioned inside corolla tubes, and may only be accessible when the majority of the petals are consumed.

Multiple linear regressions were used to determine the factors that explain variation in percentage fruit set (the continuous response variable) in each population. Beetle density, petal colour, floral display (number of flowers open simultaneously), number of conspecific plants within 1 m, and number of conspecific plants between 1 and 2 m were the fixed effects. Percentage of unripe fruits eaten by mammals was also included as a fixed effect in the Greenhorn population; mammal herbivory was absent (or nearly absent) in the other two populations (Table 1). Interactions between floral display size and conspecific plant density were also examined. To maximize the independence between local conspecific density measurements, the number of plants within 2 m only included the number of individuals between 1 and 2 m. No strong collinearity was found between independent variables, as all variance inflation factors were less than 1.85. Analyses were performed using JMP, version 9.0 (SAS Institute, Cary, NC, USA).

RESULTS

Population summary statistics

The average size of plants at China Hill (457.39 cm²) was more than three times that of plants at Cracker Gulch (137.45 cm²) and nearly twice that of plants at Greenhorn (246.89 cm²; Table 1). There were significant positive correlations between plant size and floral display ($n = 374$, $R^2 = 0.27$, $P < 0.0001$), between plant size and the total number of reproductive structures ($n = 374$, $R^2 = 0.44$, $P < 0.0001$), and between plant size and the number of fruits produced ($n = 374$, $R^2 = 0.25$, $P < 0.0001$). Thus, plants growing on China Hill produced significantly larger floral displays, significantly more reproductive structures overall and significantly more fruits than plants in the Cracker Gulch and Greenhorn populations (Table 1).

Plant density and petal colour also varied among populations. Average density of conspecific flowering plants was lowest in the Greenhorn population (1.58 at 1 m and 4.50 at 2 m), intermediate...
in the Cracker Gulch population (2.68 at 1 m and 7.43 at 2 m) and highest in the China Hill population (3.40 at 1 m and 8.65 at 2 m; Table 1). Plants in the Greenhorn population had intermediate petal colours that did not significantly differ from petal colours in the other two populations; petals produced by plants in the Cracker Gulch population, however, were significantly lighter than petals in the China Hill population (Table 1).

Florivory and granivory were most prevalent in the Greenhorn population. When observed during peak flowering, beetles had damaged 64% of the flowers on plants in the Greenhorn population and 46% of the flowers on plants in the China Hill and Cracker Gulch populations (Table 1). Mammals ate 19% of unripe fruits on plants in the Greenhorn population, but only 0–1% of unripe fruits in the China Hill and Cracker Gulch populations (Table 1).

Despite the more pronounced herbivory at Greenhorn, plants in this population had significantly higher percentage fruit set (30.79%) than plants in the China Hill (17.29%) and Cracker Gulch (12.66%) populations (Table 1).

**Florivory by beetles**

The percentage of flowers damaged on each plant was significantly positively correlated with the number of beetles on the plant (China Hill: $n = 126$, $R^2 = 0.18$, $P < 0.0001$; Cracker Gulch: $n = 125$, $R^2 = 0.09$, $P = 0.0007$; Greenhorn: $n = 125$, $R^2 = 0.08$, $P = 0.0013$). Moreover, the density of beetles on each plant remained fairly constant over time, as the number of beetles on a plant during peak flowering was indicative of the number of beetles on the same plant a few days later (China Hill: $n = 96$, $R^2 = 0.58$, $P < 0.0001$; Cracker Gulch: $n = 125$, $R^2 = 0.23$, $P < 0.0001$; Greenhorn: $n = 125$, $R^2 = 0.28$, $P < 0.0001$).

Florivorous beetles ate a variety of floral organs, including petals, stamens, stigmas and styles. When flowers with damaged petals were inspected, 29.4% had noticeable stamen damage, 6.7% were missing one or more stigma arms and 1.7% had damaged styles. The presence of stamen and style damage did not depend on the number of petals eaten (stamen: d.f. = 2, $\chi^2 = 3.88$, $P > 0.1$; style: d.f. = 2, $\chi^2 = 2.91$, $P > 0.1$; Table 2). Stigma damage, however, did increase as the number of petals consumed increased (d.f. = 2, $\chi^2 = 6.19$, $P < 0.05$; Table 2).

**Fruit set determinants**

Beetle density and floral display size had consistent significant effects on the proportion of flowers that produced a fruit (Table 3). In all three populations, percentage fruit set decreased as beetle density increased and as floral display size increased. In two of the three populations, the effect of floral display size depended on the density of nearby conspecific plants, as evidenced by the significant interaction in Cracker Gulch (d.f. = 7, 117, $\beta = 0.05 \pm 0.02$, $t = 2.53$, $P < 0.05$) and the marginally significant interaction in China Hill (d.f. = 7, 103, $\beta = 0.01 \pm 0.01$, $t = 1.91$, $P < 0.1$; Table 3). In both cases, floral display size was negatively correlated with percentage fruit set when local conspecific density was low, but positively correlated with percentage fruit set when local conspecific density was high.

Seed predation by mammals significantly decreased fruit set in the Greenhorn population (d.f. = 8, 116, $\beta = -0.38 \pm 0.04$, $t = -8.99$, $P < 0.0001$; Table 3). Petal colour did not significantly affect percentage fruit set in any population (Table 3).

**DISCUSSION**

The probability of fruit set in natural populations of self-sterile *Phlox hirsuta* was determined by multiple factors including floral display size, local conspecific density, florivorous beetle density and pre-dispersal seed predation. Interestingly, three of the four factors that explained the variation in percentage fruit set have been shown to alter the behaviour of pollinators. Traits that promote outcross pollination (i.e. higher conspecific densities and lower florivorous beetle densities) increased fruit set, while traits that promote geitonogamous self pollination (i.e. larger floral displays) decreased fruit set. Higher fruit set in individuals that avoid (or minimize) geitonogamous self pollination is expected, as the presence of self pollen grains on stigmas reduces seed set in *P. hirsuta*, especially when self pollen grains reach stigmas before outcross pollen grains (Ruane et al., 2013). Thus, traits that affect the frequencies of self versus outcross pollinations play a critical role in determining the reproductive success of this endangered species.

Floral display size was significantly negatively correlated with percentage fruit set in all three populations (Table 3). *P. hirsuta* individuals with larger floral displays, which can have up to 271 flowers open simultaneously, are more prone to geitonogamous self pollination than individuals with smaller floral displays (de Jong et al., 1992; Barrett et al., 1994; Harder and Barrett, 1995, 1996). In *P. hirsuta*, the number of flowers that open simultaneously – and therefore the degree of geitonogamous self pollination – may be a function of plant age, as new growth arises each spring from the tips of pre-existing shoots that became dry and non-photosynthetic the preceding summer. Although larger (presumably older) plants are more prone to the fitness costs associated with geitonogamous self pollination, larger plants did produce more fruits overall than smaller plants (see Results). Thus, the degree to which *P. hirsuta* individuals contribute to population growth may progressively increase as plants age, assuming seed production contributes to population dynamics (Schemske et al., 1994).

High conspecific densities mitigated – even reversed – the detrimental effects of floral display size on percentage fruit set. In two of the three populations, floral display size was negatively correlated with percentage fruit set when local conspecific density was low, but positively correlated with percentage fruit set when local conspecific density was high. Facilitative interactions among conspecifics in high-density areas not only increase

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**Table 2.** Phlox hirsuta flower parts damaged by florivorous beetles (data are separated by flowers that had 1–2, 3–4, and all 5 petals eaten; means and s.e. are presented)

<table>
<thead>
<tr>
<th>No. of petals eaten</th>
<th>n</th>
<th>% of flowers with stamen damage</th>
<th>% of flowers with stigma damage</th>
<th>% of flowers with style damage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–2</td>
<td>67</td>
<td>20.9 (5.0)</td>
<td>4.5 (2.5)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>3–4</td>
<td>66</td>
<td>34.8 (5.9)</td>
<td>3.0 (2.1)</td>
<td>3.0 (2.1)</td>
</tr>
<tr>
<td>5</td>
<td>47</td>
<td>34.0 (7.0)</td>
<td>14.9 (5.2)</td>
<td>2.1 (2.1)</td>
</tr>
</tbody>
</table>

Means sharing letters are not significantly different ($P > 0.05$).
pollinator activity (Schaal, 1978; Heinrich, 1979; Sih and Baltus, 1987; Kunin, 1993, 1997), but also alter pollinator foraging patterns and consequently the composition of pollen grains deposited on stigmas. For example, pollinators are more likely to travel between plants and less likely to travel within plants when local conspecific density is high (Antonovics and Levin, 1980; van Treuren et al., 1993; Karron et al., 1995; Ghazoul et al., 1998). Thus, in P. hirsuta and other species that experience fitness costs associated with self-pollination, high conspecific densities may increase the fitness of individuals with large floral displays by discouraging geitonogamous self-pollination and/or encouraging outcross pollination (Waites and Ågren, 2004).

In P. hirsuta, the spatial scale at which density affected fruit set was very local (i.e. within 1 or 2 m; see also Roll et al., 1997; Ghazoul et al., 1998; Colling et al., 2004; Ishihama et al., 2006). The positive correlations between local conspecific density and fruit set suggest that individuals are surrounded by genetically compatible mates (Levin, 1989; Souto et al., 2002) and that the facilitative effects of intraspecific interactions outweigh the potential negative effects of intraspecific competition for resources or pollinators (Antonovics and Levin, 1980; Rathcke, 1983; Moeller, 2004). If density continues to increase, however, it may have the opposite effect on fruit set. For example, in Nierembergia linariifolia, a self-incompatible species, plant density was positively correlated with seed set when density ranged from 0 to 12 plants m⁻², but was negatively correlated with seed set when density exceeded 12 plants m⁻² (Nattero et al., 2011). Thus, conservation strategies to increase fitness by population augmentation should focus on adding plants to low- (not high-) density areas, as isolated individuals are more likely to benefit from additional neighbours.

Florivorous beetles also affected the reproductive success of P. hirsuta. Plants within all three populations had lower fruit sets when their flowers were covered with higher beetle densities. Beetles may have decreased fruit set by consuming stigmas prior to pollen germination (Table 2) or by altering the composition of pollen grains deposited on stigmas. For example, beetles could have decreased the frequency of outcross pollination, as pollinators are less likely to visit damaged flowers (Krupnick et al., 1999; Pohl et al., 2006; Cardel and Koptur, 2010). It is also possible that beetles increased the frequency of geitonogamous self-pollination, as pollen-coated beetles were observed moving between flowers within the same plant, but seldom seen traveling between adjacent plants. Thus, when florivorous beetles do not consume stigmas, they may prevent fruit set by decreasing the frequency of outcross pollinations and/or increasing the frequency of self pollinations.

Surprisingly, average percentage fruit set was highest for plants in the Greenhorn population, which exhibited the lowest local conspecific density, the highest beetle density and the most granivory (Table 1). The relatively high fruit set by plants in the Greenhorn population could be due to a variety of factors, including higher S-allele diversity (Glemin et al., 2008), less spatial genetic structure (Rossum and Triest, 2006) and more effective pollinators (Mayfield et al., 2001; Moeller, 2005). Although the identity and abundance of insects probing P. hirsuta flowers in the China Hill and Cracker Gulch populations have been assessed (Filipski, 2005; Ferguson et al., 2006), information about the pollinator

### Table 3. Results of multiple linear regressions showing the effects of independent variables on percentage fruit set in three Phlox hirsuta populations

<table>
<thead>
<tr>
<th>Population</th>
<th>Independent variable†</th>
<th>Coefficient</th>
<th>s.e.</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>China Hill</td>
<td>Beetle density</td>
<td>-85.28</td>
<td>31.97</td>
<td>-2.67</td>
<td>0.0089**</td>
</tr>
<tr>
<td></td>
<td>Petal colour</td>
<td>-0.14</td>
<td>0.49</td>
<td>-0.30</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td>Floral display</td>
<td>-0.04</td>
<td>0.02</td>
<td>-2.59</td>
<td>0.0110*</td>
</tr>
<tr>
<td></td>
<td>Plant density (1 m)</td>
<td>0.98</td>
<td>0.42</td>
<td>2.36</td>
<td>0.0202*</td>
</tr>
<tr>
<td></td>
<td>Plant density (2 m)</td>
<td>0.29</td>
<td>0.26</td>
<td>1.14</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (1 m)</td>
<td>-0.01</td>
<td>0.04</td>
<td>-0.67</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (2 m)</td>
<td>0.01</td>
<td>0.01</td>
<td>1.91</td>
<td>0.0588+</td>
</tr>
<tr>
<td>Cracker Gulch</td>
<td>Beetle density</td>
<td>-68.79</td>
<td>33.94</td>
<td>-2.03</td>
<td>0.0449*</td>
</tr>
<tr>
<td></td>
<td>Petal colour</td>
<td>-0.20</td>
<td>0.49</td>
<td>-0.40</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Floral display</td>
<td>-0.10</td>
<td>0.04</td>
<td>-2.62</td>
<td>0.0101*</td>
</tr>
<tr>
<td></td>
<td>Plant density (1 m)</td>
<td>0.03</td>
<td>0.52</td>
<td>0.05</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>Plant density (2 m)</td>
<td>0.32</td>
<td>0.31</td>
<td>1.03</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (1 m)</td>
<td>0.05</td>
<td>0.02</td>
<td>2.53</td>
<td>0.0129*</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (2 m)</td>
<td>-0.01</td>
<td>0.01</td>
<td>-1.03</td>
<td>0.31</td>
</tr>
<tr>
<td>Greenhorn</td>
<td>Beetle density</td>
<td>-71.02</td>
<td>25.95</td>
<td>-2.74</td>
<td>0.0072**</td>
</tr>
<tr>
<td></td>
<td>Petal colour</td>
<td>-0.42</td>
<td>0.70</td>
<td>-0.60</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Unripe fruits eaten (%)</td>
<td>-0.38</td>
<td>0.04</td>
<td>-8.99</td>
<td>&lt;0.0001**</td>
</tr>
<tr>
<td></td>
<td>Floral display</td>
<td>-0.09</td>
<td>0.04</td>
<td>-2.34</td>
<td>0.0208*</td>
</tr>
<tr>
<td></td>
<td>Plant density (1 m)</td>
<td>-1.11</td>
<td>0.94</td>
<td>-1.17</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Plant density (2 m)</td>
<td>0.40</td>
<td>0.56</td>
<td>0.72</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (1 m)</td>
<td>-0.01</td>
<td>0.03</td>
<td>-0.16</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>Floral display × Plant density (2 m)</td>
<td>0.01</td>
<td>0.02</td>
<td>0.63</td>
<td>0.53</td>
</tr>
</tbody>
</table>

A positive coefficient indicates a positive relationship between the independent variable and percentage fruit set. The overall model was significant for China Hill ($R^2 = 0.26$, d.f. = 103, $F = 5.04$, $P < 0.0001$), Cracker Gulch ($R^2 = 0.14$, d.f. = 117, $F = 2.83$, $P < 0.0093$) and Greenhorn ($R^2 = 0.47$, d.f. = 116, $F = 12.90$, $P < 0.0001$).

†See footnotes to Table 1 for detailed information about each independent variable.

**P < 0.01, *P < 0.05, + P < 0.1.
community in the Greenhorn population is lacking. Certainly, the abundance and activity of pollinators that effectively transfer pollen grains between plants could explain interpopulation variation in fruit set (Wilson and Thomson, 1991; Ivey et al., 2003; Waites and Ågren, 2004). Higher percentage fruit set in the Greenhorn population may also occur if self interference is less prevalent here. For example, flowers could experience less self pollination if they have smaller stigmas and/or shorter styles, as these traits significantly decrease the number of self pollen grains autonomously deposited in this species (Ruane et al., 2013). Thus, knowledge about how other ecological, morphological, physiological and genetic traits vary within and among Phlox hirsuta populations is required to identify additional factors governing fruit set.

In summary, our results reveal that spatial variation in fruit set within P. hirsuta populations depends in part on factors that control the frequencies of self and outcross pollinations. Larger local conspecific densities and lower florivorous beetle densities – two traits that promote outcross pollination – increased fruit set, whereas larger floral displays – a trait that promotes self pollination – decreased fruit set. Interestingly, high densities of conspecific flowering plants offset – even reversed – the negative effects of floral display size on fruit set. Assuming that fecundity limits the growth of P. hirsuta populations, our results have important implications for conservation. First, population augmentation could increase fruit set if flowering conspecific plants are added near larger plants, especially those in isolated areas. Second, mammals could be excluded from the Greenhorn population during fruit development to prevent granivory (e.g. Auld and Myerscough, 1986; Ehrlén, 1992). And finally, the population sizes of florivorous beetles could be reduced during peak flowering (e.g. Bevill et al., 1999). Ultimately, manipulations that maximize outcross pollination and minimize self pollination will enhance the ability of this endangered species to produce seed-containing fruits.

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LITERATURE CITED


