

## THE CONTRIBUTION OF DISPLAY SIZE AND DICHOGAMY TO POTENTIAL GEITONOGAMY IN *CAMPANULA AMERICANA*

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An increase in floral display size may enhance fitness by increasing a plant's attractiveness to pollinators. Alternatively, a larger display may reduce fitness by increasing pollen movement within an individual. In dichogamous species the frequency of this geitonogamy also depends on floral gender ratio and pollinator response to floral gender and to inflorescence architecture. We explored the relationships of floral display size and dichogamy to potential geitonogamy in *Campanula americana*, a protandrous herb. We observed pollinators in a natural population, in which individuals differed in display size, gender ratio, and distance to conspecifics, and in experimental arrays, in which individuals differed only in display size. In both settings, bees responded to increased floral displays by increasing the number and length of foraging bouts. The number of potentially geitonogamous visits, those to female-phase flowers after male-phase flowers, also increased with display size. In addition, although proportion of flowers visited did not increase with the floral display, the proportion of geitonogamous visits did. There was no evidence that dichogamy reduced the potential for geitonogamy. The ratio of male- to female-phase flowers did not affect bee behavior, and bees did not display a gender preference. In contrast to other studies, the presentation of female-phase flowers below male-phase flowers on reproductive branches did not reduce geitonogamy. Variation in floral display size may cause the mating system to vary among populations. We found that display size varied among 12 populations and that geitonogamy may be infrequent in many populations as a result of small display sizes. Finally, within populations, the selfing rates of larger biennial *C. americana* are likely to exceed those of smaller annual individuals.

**Keywords:** geitonogamy, display size, pollinator behavior, protandry.

### Introduction

Floral display size has been called the “plant's dilemma” for insect-pollinated species (Klinkhamer and de Jong 1993). An increase in the number of flowers per plant may increase fitness by attracting more pollinators that import and export more pollen. However, increases in floral display may also incur costs from increased geitonogamy, the transfer of pollen between flowers within an individual (de Jong et al. 1993; Barrett and Harder 1996; Snow et al. 1996; Ohashi and Yahara 1999). Within-plant pollen transfer will reduce male fitness because of the loss of outcrossing opportunities by pollen that is deposited on stigmas within an individual (pollen discounting). Within-plant pollen transfer may reduce female fitness in self-incompatible plants if the presence of self pollen on the stigma reduces the access of outcross pollen to ovules. Finally, in self-compatible plants, geitonogamy will reduce both male and female fitness if selfed progeny express inbreeding depression.

The temporal separation of male and female function within a flower (dichogamy) is thought to have evolved to minimize fitness losses from self-pollination within flowers or to reduce interference between male and female functions (Lloyd and Webb 1986; Bertin 1993). However, geitonogamy is possible

in dichogamous species if pollinators visit female-phase flowers after male-phase flowers on the same plant. Inflorescence and plant level characters may reduce this potential for geitonogamy. An example is the location of female-phase flowers below male-phase flowers on an inflorescence. If pollinators forage upward, they will visit female-phase flowers prior to male-phase flowers (Darwin 1876; Best and Bierzychudek 1982) and decrease geitonogamous selfing (Harder et al. 2000). Inflorescence architecture is less structured in many dichogamous species (Rademaker et al. 1999). In these plants, patterns of pollinator movement between male- and female-phase flowers, perhaps reflecting preference for either gender (Aizen and Basilio 1998), will influence the potential for geitonogamous pollen transfer. Although several studies have demonstrated that larger display sizes increase the number of flowers visited in a foraging bout and result in more geitonogamy (Geber 1985; Hessing 1988; Klinkhamer et al. 1989; Klinkhamer and de Jong 1990; Dudash 1991; Robertson 1992; Barrett et al. 1994; Robertson and Macnair 1995; Rademaker and de Jong 1998), we know much less about the potential for dichogamy to reduce geitonogamy, especially in the common situation of loosely structured or unstructured inflorescences.

We evaluated the effect of floral display size on the potential for geitonogamy in the herbaceous plant *Campanula americana* L. (Campanulaceae). *Campanula americana* flowers are protandrous and arranged into one to many small clusters, each with female-phase flowers at the base. Pollinators move

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among clusters of flowers within a plant, providing the opportunity to evaluate geitonogamy in a dichogamous species with a loosely structured inflorescence. We quantify patterns of pollinator movement as an index of geitonogamy. Studies that have both observed pollinators and directly measured mating patterns have demonstrated that the selfing rate increases (Crawford 1984; Barrett et al. 1994; Harder and Barrett 1995; Snow et al. 1996; Vrieling et al. 1999) and the outcrossing rate decreases (Harder and Barrett 1995) as pollinators visit more flowers on a plant. Also, selfed and outcross pollination of *C. americana* flowers results in equivalent seed production (L. F. Galloway, unpublished manuscript); therefore, within-plant pollinator movement is likely to lead to geitonogamy.

We explored the relationship between dichogamy, floral display size, and potential geitonogamy by evaluating the behavior of pollinators in natural populations and experimental arrays. We first quantify diurnal patterns of floral gender expression and pollinator activity to determine whether pollen movement within plants could vary with time of day. We then evaluate whether a bee's response to display size and floral gender influences the potential for geitonogamy in a natural population. Next we describe bee response to display size in experimental arrays in which gender ratio and background flower number are constant. Last, we survey floral display sizes in 12 populations to ascertain whether variation in the potential for geitonogamy may lead to differences in mating patterns among populations. The relationship between geitonogamy and display size is of particular interest in *C. americana* because individuals grow as either annuals or biennials, and variation in display size within a population is partially attributable to life history.

## Material and Methods

### *Study Species*

*Campanula americana* is a monocarpic insect-pollinated herb. It flowers from mid-July through late August. The primary pollinators are bumblebees foraging for nectar and halictids collecting pollen (Johnson et al. 1995). The flowers are self-compatible but protandrous. The male phase is brief, with most pollen removed within 2 h of anthesis (Johnson et al. 1995; Evanhoe and Galloway 2002). Following removal of all pollen, the flower is functionally neuter until the stigmatic lobes open the next day (Shetler 1962; L. F. Galloway, personal observation). Flowers remain in female phase for 1–2 d, for a floral life of 2–3 d (Evanhoe and Galloway 2002). Flowers are located in compact inflorescences at reproductive nodes on the main stem and side branches. Typically a single flower is open at each node, with flowers at one to six (mean  $\pm$  SE,  $3.05 \pm 0.44$ ) adjacent nodes opening simultaneously. Anthesis progresses distally along branches; therefore, the lower flowers in blooming clusters are in female phase, whereas the newly opened flowers toward branch tips are in male phase. The number of clusters of flowers increases with branch number and branch length.

### *Diurnal Patterns of Gender Expression*

Diurnal patterns of gender expression were quantified in two populations (RT700 and RT613, both 4.5 km from the Mountain Lake Biological Station [MLBS], Giles, Va.) during the peak flowering season. We counted the numbers of flowers in the male, female, and neuter phases every 3 h from 0600 to 1800 hours on 20 randomly selected plants in each population. Pollinator activity was monitored at each census time by counting the number of pollinators to visit a cluster of ca. 270 flowers during 15 min (RT700 only).

### *Pollinator Response to Display Size (Nature)*

The effect of floral display size on pollinator behavior was determined by observing pollinators on 57 plants in the RT700 population. The plants were chosen to include a range of floral display size. Each plant was observed for 15 min between 1230 and 1530 hours during peak flowering. Ten plants were observed each day, except for the final day, on which we observed seven plants. Before each observation we counted the number of flowers in each gender phase. Because previous studies have demonstrated that plant density influences pollinator behavior (e.g., Cibula and Zimmerman 1984; Klinkhamer and de Jong 1990; Kunin 1993), we also quantified proximity to neighboring *C. americana* by measuring the distance to the three closest conspecifics for each individual.

During each observation period we recorded the number and gender sequence of flowers visited by each bee and noted bee movements between clusters of flowers. These data were used to calculate six variables: the total number of bees that foraged on a plant during the 15-min interval, the mean number of flower clusters visited per bee, the mean number of flowers visited per bee ("visits"), the proportion of flowers visited ("proportion visited"), the mean number of female-phase flowers visited after a male-phase flower during a foraging bout ("geitonogamous visits"), and the proportion of female-phase flowers that received geitonogamous visits ("geitonogamous proportion visited"). Evaluation of the number and proportion of geitonogamous visits considered only plants with both male- and female-phase flowers. The number of bees and their behavior were analyzed using analysis of covariance (ANCOVA), with day of observation as a categorical variable and floral display size, mean distance to the nearest *C. americana*, and the proportion of flowers in the female phase as continuous variables. Analysis of plant means resulted in data that met the assumptions of ANCOVA when transformed. Means are reported ( $\pm$ SE) throughout.

### *Pollinator Response to Display Size (Arrays)*

Experimental arrays were also used to test the effect of floral display size on pollinator behavior. Haphazardly selected *C. americana* were transplanted from natural populations before flowering. When plants flowered, arrays were constructed with a "focal" plant in the center, surrounded by six "background" plants arranged in a hexagon, with 1 m between individuals. Flowers were removed so that focal plants had 3, 9, or 21 flowers, and background plants had five flowers each. The gender ratio of all plants was adjusted to the 1 male : 2 female typical of natural populations (see "Results"). In each array,

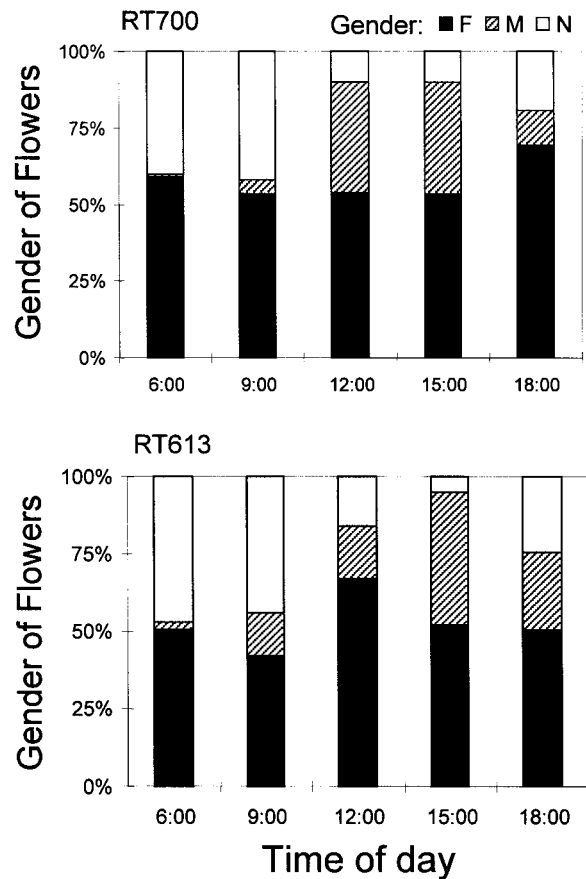


Fig. 1 Percent of flowers in female (F), male (M), and neuter (N) phases during a day in two *Campanula americana* populations.

the number and gender sequence of flowers visited on the focal plant was recorded for five bumblebees (Hymenoptera: *Bombus*). Halictid bees that visited during observation periods were included; their behavior did not differ from *Bombus* (results not shown). A total of 38 arrays, 12–13 of each treatment level, were observed during 21 d within the natural flowering season. The arrays were located ca. 100 m from the closest *C. americana* population.

#### Population Variation in Display Size

Floral display size was assessed in all roadside populations (a common habitat) of *C. americana* within 15 km of MLBS. The 12 populations were found on south-facing slopes (aspect  $188^\circ \pm 4^\circ$ , slope  $37^\circ \pm 3^\circ$ ), ranging from 600 to 1170 m in elevation. The number of open flowers was counted on ca. 25 individuals along transects through the center of large populations and on all individuals in small populations ( $N < 40$ ). Populations were visited twice, and flower counts closest to the peak bloom period were used.

### Results

#### Diurnal Patterns of Gender Expression

Changes in floral gender during the day in two natural populations were analyzed using a repeated-measures ANOVA on

percent female. On average, at least 75% of the sexually functional flowers were in female phase (population  $F_{1,31} = 0.21$ ,  $P = 0.65$ ; fig. 1). However, gender expression changed significantly during the day ( $F_{4,124} = 14.93$ ,  $P < 0.001$ ), with few male-phase flowers during the morning but similar numbers of male- and female-phase flowers during the afternoon. Earlier opening of new male-phase flowers at the RT700 site caused the temporal pattern of gender expression to differ between the populations ( $F_{4,124} = 6.21$ ,  $P < 0.002$ ; fig. 1). An additional survey in the RT700 population revealed little variation in diurnal patterns of gender expression over the season ( $F_{1,35} = 1.54$ ,  $P = 0.22$ ). Bee activity peaked during the afternoon when the gender ratio was closest to equal (fig. 2).

#### Pollinator Response to Display Size (Nature)

Pollinators were observed on plants that had 1–90 open flowers (median 12, interquartile range 4–30) and were 0.15–5.0 m from the nearest *Campanula americana* (median 0.9 m, interquartile range 0.4–1.7 m). Floral display size did not vary with nearest neighbor distance ( $r = -0.03$ ,  $P = 0.81$ ,  $n = 57$ ). On average, eight bees visited a plant during a 15-min observation period (range 0–28). Overall, 96% of the 465 bees observed in the natural population were *Bombus* (*B. affinis* and *B. bimaculatus*), and the remaining 4% were Halictids. Pollinator number, the number of flower clusters visited, and the number of flowers visited all increased with display size (table 1; fig. 3). The proportionate increase in these variables was less than the increase in display size (nonstandardized  $\beta_{\text{pollinators}} = 0.65$ ,  $\beta_{\text{clusters}} = 0.42$ ,  $\beta_{\text{visits}} = 0.41$ , all  $< 1$ , cf. Klinkhamer et al. 1989). However, the total number of flowers visited (number of bees  $\times$  number of visits per bee) increased almost exactly in proportion with display size (summed  $\beta = 1.06$ ). As a consequence the proportion of flowers visited varied little with the size of the floral display (table 1).

The proportion of flowers in the female phase on the observed plants ranged from 0 to 1, with an average of  $0.48 \pm 0.03$ . There was a slight negative association between the proportion of female-phase flowers and display size ( $r = -0.21$ ,  $P = 0.12$ ,  $N = 57$ ). However, there was little evidence that bees biased visits toward either gender. A gender bias would be expected in the sequence of visits if bees forage upward because they would visit female-phase flowers at the base

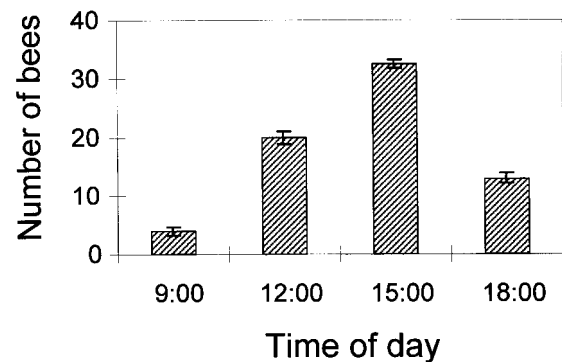
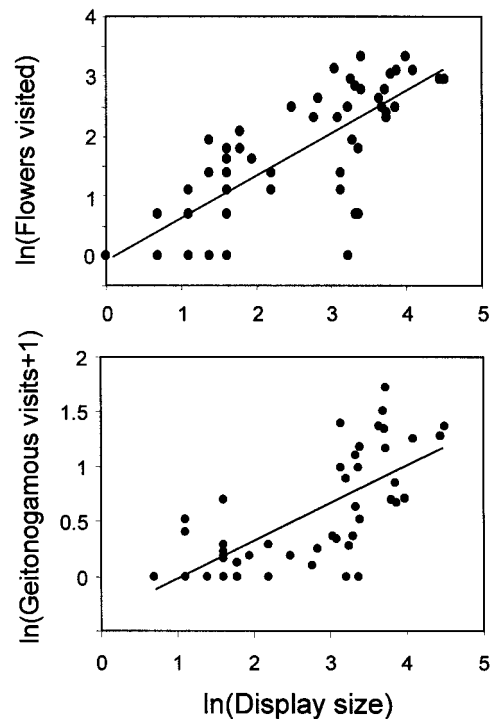


Fig. 2 Mean (SE) number of bees to visit a group of ca. 270 *Campanula americana* flowers during a day.

of clusters before visiting male-phase flowers. In this case, a regression of the proportion of female-phase flowers on the frequency with which female-phase flowers were visited first in clusters would have a positive intercept, indicating that females are overvisited in the first flower (the slope is expected to be near unity if the gender ratio does not influence the extent to which female-phase flowers are visited first in clusters). However, the intercept of this regression did not differ significantly from zero (female first = 1.31 proportion female – 0.14,  $P < 0.001$ ,  $R^2 = 0.59$ ), revealing that female-phase flowers received the first visit to a cluster no more frequently than expected given the gender ratio of the plant. In addition, no aspects of pollinator behavior were associated with the proportion of flowers in the female phase (table 1). Finally, regression demonstrated that the ratio of bee visits to female-phase flowers relative to visits to all flowers did not change with plant size (visits to females = 1.01 total visits – 0.99,  $P < 0.001$ ,  $R^2 = 0.61$ , both variables ln-transformed).

Geitonogamy is possible only if a pollinator visits a female-phase flower after a male-phase flower on the same plant. The potential for pollen movement within plants, estimated by the number of “geitonogamous” visits, increased with display size (table 1; fig. 3). The proportion of geitonogamous visits also increased with display size, in contrast to the proportion of flowers visited (table 1). Hence, the potential for geitonogamy was greater in plants with larger floral displays.

Relatively isolated plants received fewer pollinator visits, but each bee visited more flower clusters and more flowers than they did on plants with close neighbors (table 1). However, the overall proportion of flowers visited was not influenced by *C. americana* density (table 1). There was also a positive relationship between distance to conspecifics and the number and proportion of geitonogamous visits, indicating that isolated plants experience a greater potential for geitonogamous pollen movement.



**Fig. 3** The number of flowers visited and of potentially geitonogamous visits by bees to plants displaying different numbers of flowers in a natural *Campanula americana* population. Least square regression lines are included. See table 1 for analysis.

#### Pollinator Response to Display Size (Arrays)

When plant size, background flower number, and gender ratio were held constant, bees visited more flowers and more female-phase flowers after male-phase flowers on plants with

**Table 1**

**The Effects of Floral Display Size, Distance to Conspecific *Campanula americana*, Gender Ratio, and Day of Observation (a Blocking Factor) on Pollinator Behavior**

| Dependent variable                           | Display size |           | Distance |                   | Proportion female: <sup>b</sup> <i>F</i> | Day: <i>F</i>     |
|--|--------------|-----------|----------|-------------------|--|-------------------|
|  | $\beta'$     | $F^a$     | $\beta'$ | <i>F</i>          |  |                   |
| Number of pollinators                        | 0.74         | 123.14*** | -0.22    | 8.90**            | 0.68                                     | 6.43***           |
| Number of clusters visited                   | 0.78         | 82.05***  | 0.28     | 8.16**            | 0.64                                     | 0.25              |
| Number of flowers visited                    | 0.72         | 62.98***  | 0.31     | 9.12**            | 0.00                                     | 0.95              |
| Number of geitonogamous visits <sup>c</sup>  | 0.66         | 48.95***  | 0.26     | 6.05*             | 3.11 <sup>+</sup>                        | 2.07 <sup>+</sup> |
| Proportion flowers visited <sup>d</sup>      | 0.15         | 1.42      | 0.11     | 0.52              | 0.84                                     | 4.53**            |
| Proportion geitonogamous visits <sup>b</sup> | 0.61         | 36.95***  | 0.20     | 3.16 <sup>+</sup> | 1.72                                     | 4.18**            |

Note. Each variable was ln-transformed (except where noted) and analyzed with a separate ANCOVA, with day of observation as a fixed effect. Standardized partial regression coefficients not given for proportion female since no *F*-tests were significant.

<sup>a</sup> Display size, distance, proportion female  $df_{num} = 1$ , day  $df_{num} = 5$ ;  $df_{error} = 40$  to 43.

<sup>b</sup> Not transformed.

<sup>c</sup>  $\ln(x + 1)$ -transformed.

<sup>d</sup> Square root transformed.

<sup>+</sup>  $0.05 < P < 0.10$ .

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

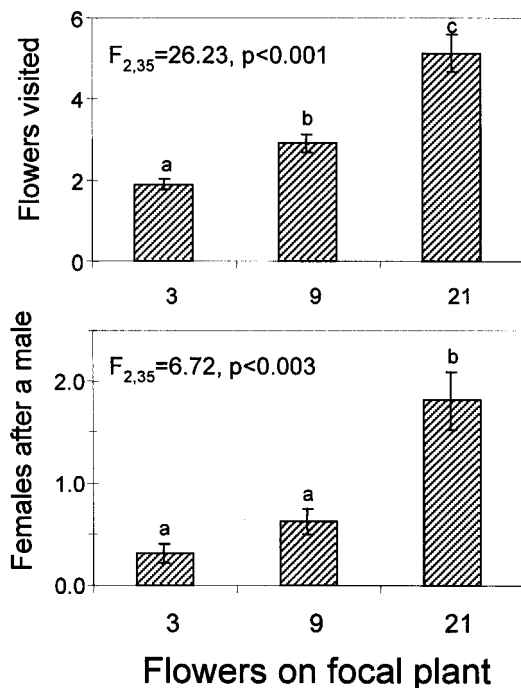
larger floral displays (fig. 4). Increases in display size did not result in proportionally more flowers visited or geitonogamous visits. However, the number of geitonogamous visits increased more with display size than did flowers visited. On average, bees visited less than one female-phase flower after a male-phase flower for display sizes of 3 and 9, so typical foraging bouts on small displays would not cause geitonogamy.

#### Population Variation in Display Size

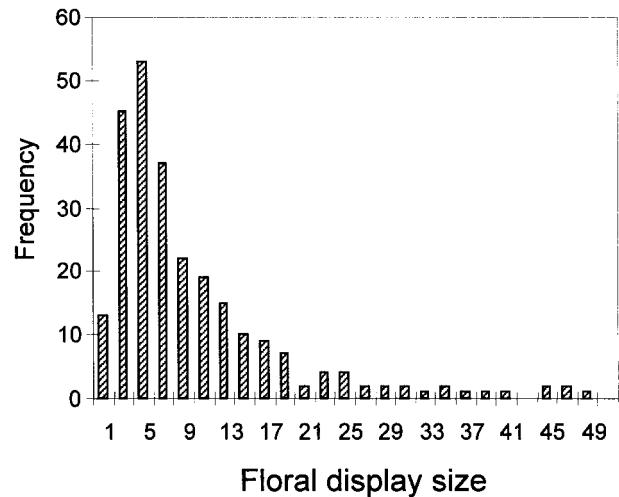
Over 12 populations, display size varied log-normally and ranged from 0 to 63 open flowers (fig. 5). A one-way ANOVA found display size ( $\ln[x + 1]$  transformed) varied significantly among sites, with population means ranging from 5.6 to 20.5 open flowers per plant ( $F_{11,249} = 5.86$ ,  $P < 0.001$ ).

#### Discussion

Floral display size varied extensively among individuals in *Campanula americana*. Bees responded to this variation by increasing the number of foraging bouts and the number of flowers visited per plant on plants with larger displays. Similar patterns of pollinator response to increased floral display size have been documented for a number of other species (Geber 1985; Hessian 1988; Klinkhamer et al. 1989; Klinkhamer and de Jong 1990; Dudash 1991; Robertson 1992; Barrett et al.



**Fig. 4** Mean (SE) number of flowers visited and potentially geitonogamous visits by bees to *Campanula americana* in experimental arrays. Display size of the observed individual was manipulated to 3, 9, or 21 flowers, whereas the background plants each had 5 flowers. Results of one-way ANOVA (visits  $\ln$ -transformed, geitonogamous visits square root transformed) are given for each variable; means that differed at  $\alpha = 0.05$  using a Tukey multiple comparison test are indicated by a different letter.



**Fig. 5** Floral display size for randomly selected plants in 12 *Campanula americana* populations. Four plants (not shown) had between 49 and 63 flowers.

1994; Robertson and Macnair 1995; Goulson et al. 1998; Rademaker and de Jong 1998). As with most species that have been examined, increases in flower number per plant were not fully matched by increases in the number of pollinators attracted or of flowers visited per pollinator. As a result, individual flowers did not receive more visits as display size increased. Therefore, although male and female reproductive success is expected to increase with display size, there is little evidence of increased efficiency in pollination with larger displays (*sensu* Robertson and Macnair 1995; Ohashi and Yahara 1999). In addition, any gains in fitness may be reduced by the increased geitonogamy typically found when pollinators visit more flowers on an individual (de Jong et al. 1993; Barrett and Harder 1996; Snow et al. 1996).

With dichogamous flowers, geitonogamy requires a pollinator to visit female-phase flowers after a male-phase flower on the same plant. In both natural and experimental populations of *C. americana*, dichogamy did not prevent potential within-plant pollen transfer. The number of flowers in female phase visited after one in male phase increased with floral display size. For example, the array experiment revealed that only about half of the bee visits to plants with three or nine flowers could have caused geitonogamy. In contrast, every visit to plants with 21 flowers involved movements from a male-phase flower to at least one female-phase flower on the same plant. The magnitude of the treatment effect may partially reflect the fact that focal plants with 21 flowers had four times the flower number of the background plants. Previous work has demonstrated that pollinator behavior is context dependent, and focal plants receive more visits when they have many more flowers than the background plants (Harder and Barrett 1995). The proportion of visits with the potential for geitonogamy also increased with the number of flowers in the display, whereas the proportion of flowers visited did not change with display size. Therefore, even though flowers in large displays do not receive more visits, the visits are more likely to result in geitonogamy.

The display structure of *C. americana* does not reduce the potential for geitonogamy. A number of studies have demonstrated that bees move upward on inflorescences during a foraging bout (e.g., Corbet et al. 1981; Best and Bierzychudek 1982; Hodges 1985; Richardson and Stephenson 1989; Barrett et al. 1994), and therefore the location of female-phase flowers below male-phase flowers will reduce selfing (Harder et al. 2000). Female-phase flowers are at the base of floral clusters in *C. americana*. However, there was no evidence that bees habitually begin foraging at the base of clusters and then move upward. Female-phase flowers were visited first in clusters with the same frequency with which they occurred on plants, regardless of the display size. Therefore, structure within floral clusters does not reduce geitonogamy in this species. In addition, bees move between clusters of flowers more frequently on plants with more flowers, and movement between clusters may result in geitonogamy regardless of within-cluster movement patterns. If true for other species with loosely structured or unstructured inflorescences, these results indicate a greater role for dichogamy in reducing interference between male and female function (Lloyd and Yates 1982; Lloyd and Webb 1986) than in decreasing geitonogamous selfing.

An association between plant gender and display size may influence the potential for geitonogamy in plants with dichogamous flowers. However, the ratio of male- to female-phase flowers did not vary with display size in *C. americana*. On average, plants had almost twice as many female- as male-phase flowers. Plant gender did vary during the day from strongly female biased in the morning to close to equal in the afternoon. Pollinators visited most frequently during the afternoon; therefore, pollen movement within and between individuals is likely to be most frequent when plants display near equal numbers of female- and male-phase flowers. Bee preference for either gender could influence the potential for geitonogamy, but the gender ratio of flowers on a plant did not affect bee behavior during midday. Bees also visited flowers of each gender in proportion to their frequency on all size displays. Therefore, pollinator preference is not likely to influence rates of geitonogamy. In contrast, bees preferred male-phase flowers to female-phase flowers in *Echium vulgare* (Rademaker et al. 1999).

Does *C. americana* typically display enough flowers that within-plant pollen movement is likely? The survey of display size in natural populations found that 65% of plants had  $\leq 9$  flowers (fig. 5). On plants with these display sizes, at least half of bee visits will not result in geitonogamy. In contrast, only 4.2% of randomly selected plants had displays of  $\geq 21$  flowers that resulted in an average of 1.5 visits to female-phase flowers after a male on the same plant. Although within-plant pollen movement could occur when a plant has as few as one male- and one female-phase flower, it is likely to occur on most bee visits less than a third of the time (plants with  $> 9$  flowers), indicating that geitonogamy may be relatively rare in natural *C. americana* populations. Furthermore, 10 of the 12 populations surveyed had a median display size of  $\leq 9$ , indicating that many populations experience relatively little geitonogamy. In the remaining populations, geitonogamy may occur commonly. Although information on the number of visits per flower, pollen carryover, and the relative siring ability of self

and outcross pollen are also necessary to evaluate potential selfing rate (Robertson 1992), differences in display size are likely to cause mating patterns to vary among populations. Variation among populations in geitonogamy is likely to occur in most self-compatible species, as floral display size often varies with plant size among populations. This expectation is supported by variation in outcrossing rates among populations (Schemske and Lande 1985; Barrett and Husband 1990; Godt and Hamrick 1991; although other ecological and morphological factors are also expected to contribute to this variation).

Factors other than floral display size can affect mating patterns. In the natural population, although plants received fewer foraging bouts as distance to conspecifics increased, the number of flowers visited and the probability of geitonogamy were greater. Therefore, for a given display size, isolated individuals probably experience more selfing. Similar patterns of pollinator behavior have been shown in other systems (Klinkhamer et al. 1989; Klinkhamer and de Jong 1990; Karron et al. 1995; Mustajarvi et al. 2001). In *C. americana*, the association of pollinator behavior with floral display size was stronger than that with distance (greater  $\beta$ ), indicating that changes in display size influence mating patterns more than relative isolation. However, this pattern may vary among species (Mustajarvi et al. 2001).

Pollinator response to variation in floral display size may lead to an interaction between mating system and life history in *C. americana*. Germination time determines life history schedule in this species (Baskin and Baskin 1984). Seeds that germinate in the autumn are winter annuals and flower the following summer, whereas those that germinate in the spring exhibit a strict biennial life history and flower the summer of their second year. Biennial *C. americana* display more flowers and produce more fruit than annual individuals (Wardle 1995; L. F. Galloway, unpublished data). The pollinator behavior reported here indicates that geitonogamy is more likely in individuals with larger floral displays. As a consequence, biennials are likely to self more than annuals. Offspring of self-pollinations have delayed germination, reduced survivorship, and smaller aboveground biomass than do outcrossed siblings (L. F. Galloway, unpublished data). To date, studies of the maintenance of life history variation in this species have focused on differential survivorship and fecundity (Wardle 1995, 1998). The results presented here indicate that differences in the mating patterns between the two life histories could also influence offspring quality. To fully understand *C. americana*'s variable life history it will be necessary to evaluate the reproductive consequences of the size differences between the life histories.

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