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SEED PRODUCTION AND INSECT VISITATION RATES IN *HESPERIS MATRONALIS* ARE NOT AFFECTED BY FLORAL SYMMETRY

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In the past decade, field manipulation and pollinator choice experiments utilizing arrays of natural and artificial flowers have yielded mixed results with respect to whether symmetric flowers receive higher visitation rates or produce more seeds compared to asymmetric flowers. In this article, we test the hypothesis that deviations from perfect floral symmetry result in decreased seed production and reduced rates of insect visitation. We performed a floral manipulation experiment in two concurrent years with *Hesperis matronalis* (Brassicaceae) to investigate how seed production per fruit was linked to floral symmetry. In addition, we performed two replicated array experiments using model plants and flowers based on *H. matronalis* to investigate whether insects make decisions to visit plants on the basis of floral symmetry and whether insects use floral symmetry as a cue to discriminate among flowers within plants. We find no clear evidence that deviations from perfect floral symmetry affect insect visitation rates to plants or flowers within a plant and no clear association between floral symmetry and seed production. However, our array experiments suggest that insects use flower size as a primary cue to discriminate among plants but not among flowers within a plant.

Keywords: experimental array, *Hesperis matronalis*, flowers, pollination, symmetry.

Introduction

The degree to which floral symmetry is an adaptive feature of angiosperms remains questionable. Møller and Eriksson (1994) showed that many species of plants have substantial intraspecific variation in the level of relative asymmetry in flowers, and subsequent studies have shown that some of this variation in asymmetry has a genetic basis (review in Møller and Swaddle 1997; Møller and Thornhill 1997). Observed deviations from perfect floral symmetry might reflect developmental instability and ultimately affect the reproductive performance of plants (review in Møller and Shykoff 1999; Møller 2000). This association between floral symmetry and plant fitness could manifest itself in several ways. If floral symmetry indeed reflects developmental instability, then plants that make relatively asymmetric flowers might also have relatively poorer rewards for pollinators (Møller 1995; Møller and Eriksson 1995) or perhaps have relatively low-quality pollen or ovules (Møller 1996). Pollinators might also visit asymmetric flowers less frequently than symmetric flowers because of an innate preference for symmetry (Giurfa et al. 1996; Lehrer 1999). In addition, negative correlations have been observed between size and symmetry (Møller and Eriksson 1994; Møller 1995); therefore, if insects make visitation decisions primarily on the basis of floral size (Bell 1985; Young and Stanton 1990; Stanton and Preston 1998), asymmetric flowers may be discriminated against.

Although there have been few studies investigating how variation in floral symmetry is associated with variation in traits involved in pollinator rewards or reproductive performance, there is a growing body of work on whether pollinators discriminate against asymmetric forms. Most studies have either manipulated floral symmetry in the field and assessed some component of fitness (e.g., seed production, pollinator visitation rates) or utilized model flowers to quantify pollinator preferences through differential visitation rates. However, the combined results of these studies are inconclusive. Utilizing an experimental manipulation approach, Møller (1995) showed that asymmetric *Epilobium angustifolium* (Onagraceae) flowers received fewer bumblebee visits than control or symmetric flowers. However, Midgley and Johnson (1998) found that manipulating the symmetry of petal markings in *Gorteria diffusa* (Asteraceae) did not affect insect visitation rates. In *Myrmecophila tibicinis* (Orchidaceae), there was a trend suggesting that increased floral asymmetry was associated with a decrease in male and female reproductive success; however, these trends were not statistically significant (Malo et al. 2001). Similarly, Frey et al. (2005) showed that neither moderately nor severely asymmetric treatments affected seed production in *Impatiens pallida* (Balsaminaceae). Experiments utilizing model flowers have also yielded conflicting results. For example, Møller and Sorci (1998) found that pollinators discriminated against asymmetric models, but West and Laverty (1998) showed that bumblebee behavior in patches of artificial flowers was unaffected by floral symmetry.

In this article, we report data from three experiments that investigate the adaptive nature of floral symmetry in *Hesperis matronalis* (Brassicaceae). In our first experiment, we manipulated the degree of floral symmetry on replicate plants in two concurrent field seasons and asked whether there was an association between the degree of floral symmetry and seed

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production per fruit. We expected that our field manipulations might affect the seed production of flowers by rendering them less attractive to pollinators, affecting the efficacy of pollination, or both. In addition, we performed two separate array experiments in the field utilizing artificial plants to determine whether insect visitation rates covaried with floral symmetry. We chose to use carefully constructed model plants and flowers designed to replicate *H. matronalis* instead of naturally occurring plants for two reasons. First, the models allowed us to control every aspect of the phenotype and let us directly test whether insect visitation rates were affected by symmetry without other confounding factors (e.g., flower number, flower size, height, nectar quality, plant height, and scent). Second, we found it impractical to use naturally occurring flowers in our model plants because a single plant rarely produced enough first-day flowers to use throughout an array. Rather than using flowers from multiple sources, which would introduce substantial variation, we chose to use model flowers that could be uniformly mass-produced. Our first array experiment contained replicate model plants that bore one of four flower model treatments. These data allowed us to test whether insect visitors utilized floral symmetry as a cue to discriminate among plants. The second array experiment contained replicate model plants that each consisted of all four flower model treatments. These data allowed us to test whether pollinators preferred symmetric model flowers over asymmetric model flowers within a particular plant. Our design for the array experiment is unique in that we took great care to construct plant models that resembled *H. matronalis* and placed our experimental arrays within a population of flowering *H. matronalis* plants. Our combined results show that deviations from perfect floral symmetry do not affect seed production in this species and that insect visitors do not discriminate against model plants containing asymmetric flowers or against asymmetric flowers within model plants.

Material and Methods

Study System

Dame's rocket (*Hesperis matronalis*) is a member of the mustard family (Brassicaceae) native to Eurasia (Choukas-Bradley 2004). Originally introduced from Europe as an ornamental garden plant, it has escaped and spread though eastern North America (Cox 1985; Choukas-Bradley 2004). Plants generally range from 0.3 to 1.0 m in height, bloom from May through July in central New York, and have four rounded, cross-shaped petals that can be pink, purple, white, or variegated (Chapman et al. 1998; Choukas-Bradley 2004; F. M. Frey, personal observation). Flowers generally range from 1 to 4 cm in width, are arranged in terminal clusters, and are fragrant in the evening hours (Cox 1985; Choukas-Bradley 2004; F. M. Frey, personal observation). Fruits mature ca. 1 mo after flowering and can grow up to 10 cm long (Cox 1985; F. M. Frey, personal observation). The plants used in this experiment were either white or pink flowered and were located on the Colgate University ski hill in areas of brush bordering forests.

Manipulation Experiment

Because it is not known whether pollinators are required for seed set in *H. matronalis*, we first performed a bagging experiment. On June 9, 2005, one flower on each of 20 plants was bagged with a thin plastic mesh prior to anther dehiscence. Bags were tied off with a thin piece of marking wire to prevent pollinator visitation. On June 27, 2005, we returned to these plants, removed the mesh covering, and checked for fruit and seed production in the field. None of the bagged flowers produced any seeds. Therefore, we concluded that pollinators are required for seed set in this species.

To investigate whether and how floral symmetry variation affects female reproductive success, we performed a series of four floral manipulations. During the second week of June in 2005 and 2006, we marked plants in the field with an aluminum tag and flag ($n = 99$ and $n = 100$, respectively). Neighboring unpollinated flowers on an inflorescence were pseudorandomly selected for the control, symmetric, asymmetric, and severely asymmetric treatments and marked with a thin piece of colored wire (fig. 1). Control flowers were marked but otherwise were not manipulated. We removed 50% of the area from a single petal for the asymmetric treatment and removed 12.5% of each of the four petals in the symmetric treatment. Therefore, the symmetric and asymmetric treatments removed the same amount of floral area. The severely asymmetric treatment was to remove an entire petal. Because the fruits of this species dehisce somewhat unpredictably, we had to assess seed production before seeds were entirely mature. At the end of June in both years, we returned to the marked flowers and counted the number of maturing seeds in each fruit. Preliminary work had shown that a careful survey at 2 wk following pollination was sufficient for reliably assessing ultimate seed production per fruit (F. M. Frey, personal observation).

Array Experiments

We investigated pollinator preferences for symmetry through the direct observation of pollinator visitation in two model array experiments. In 2005 an array of replicate model plants that resembled *H. matronalis* was constructed, and each bore one of four flower model treatments. In 2006 the array of replicate model plants each bore all four treatments. These arrays allowed us to test whether floral symmetry was used by visiting pollinators to discriminate among plants and to test whether pollinators preferred symmetric model flowers over asymmetric model flowers on individual plants.

To make the model flowers' petals, we first made a series of identical plastic templates similar in size to natural *H. matronalis* petals (ca. 1.1 cm long). Because the templates were easier to manipulate than real petals, they were made so that they maintained the original *H. matronalis* petal shape. Each template was then manipulated to create the control, symmetric, and asymmetric treatment templates. The control template was digitally photographed and was measured using an image analysis program (Motic Images Advanced 3.0, Micro-Optic Industrial Group) to find its area (43.24 mm^2). Then the symmetric and asymmetric petal templates were manipulated so their area was 6.25% and 25% smaller than the control, respectively, while maintaining the shape of the petal.

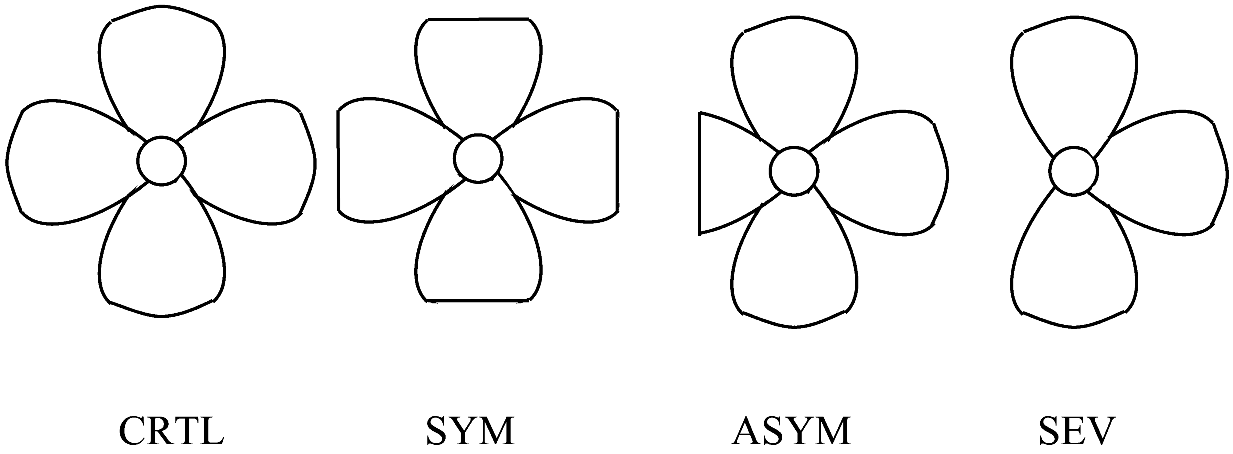

Fig. 1 Schematic representation of experimental manipulations on *Hesperis matronalis* flowers. The labels *CRTL*, *SYM*, *ASYM*, and *SEV* denote the control, symmetric, asymmetric, and severely asymmetric treatments, respectively.

The final area of the symmetric and asymmetric petal templates was 40.91 and 32.44 mm^2, respectively, which was within 1% of the final intended area.

The three templates were then used to trace petals onto 80-lb drawing paper. The petals were cut out and painted pink with a mixture of white and red oil paint. Qualitatively, the painting treatment mimicked the shade of pink present in our population. It is important to note that insects have a different visual system compared to that of humans and that our use of "pink" refers to the human perceptual experience (Briscoe and Chittka 2001; Kevan et al. 2001). The same mixture was used for all petals made within the same year, with brushstrokes going from the center of the flower out. Once dry, petals were rubber cemented onto the rim of open green Eppendorf tubes (0.5 mL) in an evenly spaced, overlapping pattern mimicking that of *H. matronalis* petals. Control flowers were made from four control petals, and symmetric flowers were made from four petals that had 6.25% of their area removed. As a result, symmetric flowers had 6.25% less total area than the control flowers. Asymmetric flowers were made from three control petals and one petal that had 25% of its area removed. Therefore, symmetric flowers and asymmetric flowers both had the same amount of total area removed relative to the control (6.25%), but this removal was distributed differently. Severely asymmetric flowers were made from three control petals and had an empty space where the missing fourth petal would have been. As a result, severely asymmetric flowers were 25% smaller than the control and 18.75% smaller than the symmetric and asymmetric flowers.

Each of the 16 model plants was made from a 3-ft wooden dowel that was painted light green with oil paint. Flowers were attached to each plant using ca. 17-cm sections of green 22-gauge wire through holes that were drilled near the top of the dowels in an alternating pattern. One end of each wire was looped to hold an Eppendorf tube, and the opposite end of each piece was threaded through a hole and wrapped around the dowel.

Each plant had six 5-in leaves in an alternating three-leaf spiral pattern, which is similar to *H. matronalis* in the field. A leaf template was made from a plant in the field and was used to create individual leaves from 140-lb watercolor paper using a combination of Fiskars paper edgers (Fiskars Brands, Madison, WI) and scissors. Leaves were painted with the same green oil paint as the stems, with brushstrokes in the direction of base to tip, and attached to the dowels with glue and green tape. In 2006, we attached leaves directly to the dowels using green 22/24-gauge wire. We drilled holes into each leaf along the "midrib" near the center and base and also into the dowels at the proper position. The wire was threaded through each leaf and its respective dowel hole and then wrapped around the dowel to better secure the leaves.

In 2005 these model plants held six flowers each, and four plants were assigned to each treatment: control, symmetric, asymmetric, and severely asymmetric. The location of each treatment within the 4 × 4 array was assigned using a random number generator. Plants were set into the ground ca. 0.4 m apart in a population of *H. matronalis* on the Colgate ski hill. Eppendorf tubes were then each filled with 0.55 mL of a 30% sucrose solution to simulate nectar. Arrays were watched for at least 1 h between 1030 and 1700 hours. We recorded the number of dipteran, hymenopteran (excluding ants), and lepidopteran visits to each plant. A visit was defined as landing on the top of a model flower, and we recorded all visits made by an insect in the array. Arrays were always constructed with entirely new petals to prevent the effects of odor marking. Eppendorf tubes were sometimes reused after cleaning. Ca. 11 h was required to prepare materials for one array, and ca. 1 h was required to set up an array in the field. We were able to complete eight arrays on sunny days between June 20 and July 15.

In 2006 the same model plants were used, but they held four flowers, one of each treatment: control, symmetric, asymmetric, and severely asymmetric. The four flowers were randomly located on each plant within the 4 × 4 array. The same location and ca. 0.55 mL of a 30% sucrose solution were used again. Arrays were watched for at least 1 h between 1200 and 1630 hours. We recorded the number of dipteran, hymenopteran (excluding ants), and lepidopteran visits to each flower and used fresh petals and Eppendorf tubes for each array. Ca. 6.5 h was required to prepare materials for one array and ca.

45 min to set up an array in the field. We were able to complete 12 arrays on sunny days between June 13 and July 1.

Statistical Analyses

In both years of the manipulation experiment, deer trampling and falling branches dramatically reduced our sample size. When we retrieved fruits to count seed production, only 53 plants (2005) and 71 plants (2006) still contained all four treatments as indicated by the marking wires. We used a one-way ANOVA to ask whether total seed production per plant for each of the four manipulations differed between years. We used a three-way ANOVA with year, treatment, and floral color as fixed factors to assess variation in seed production per fruit. Following the results of this analysis, we used separate one-way ANOVAs with post hoc Tukey tests in each year to test whether our experimental manipulations affected seed production.

For each of the array experiments, we used heterogeneity *G*-tests to test the null hypothesis that the observed distribution of visits to each of the four treatments was random. The heterogeneity *G*-test is a powerful tool for analyzing replicated experiments such as ours because it provides a measure of whether the outcomes of the replicates are homogeneous and whether the pooled frequencies significantly differ from the random expectation (Sokal and Rohlf 1995). If insects discriminated among plants (2005 array experiment) or among flowers within a plant (2006 array experiment) on the basis of floral size and symmetry, we predicted that the results would follow the alternative hypothesis of control > symmetric > asymmetric > severely asymmetric. To explicitly test whether insects discriminated on the basis of symmetry alone, we also tested the null hypothesis that the distribution of visits to the symmetric and asymmetric treatment groups was random in each experiment. These additional tests allowed us to test the prediction that symmetric > asymmetric (flowers of the same size but different symmetry).

Results

In the manipulation experiment, total seed production per plant (measured as the total number of seeds produced in the four treatments) did not vary between years ($F_{1,123} = 1.899$, $P = 0.171$). There was no significant main effect of treatment, year, or floral color in the three-way ANOVA that considered variation in seed production per fruit; however, there was a strong interaction effect between treatment and year (table 1). Therefore, we looked at the data separately for both years. In both 2005 and 2006, there was a strong effect of the floral manipulation treatment on seed production per fruit (2005: $F_{3,211} = 3.221$, $P = 0.024$; 2006: $F_{3,283} = 6.675$, $P < 0.001$), but this effect was different each year. In 2005, the average seed production of the control, symmetric, and asymmetric treatment groups was relatively high compared to that of the severely asymmetric treatment group (fig. 2*A*), and the only statistically significant difference was between the control and the severely asymmetric treatment groups. In 2006, this trend was reversed. The average seed production of the control treatment group was significantly lower than the other three treatment groups, which all had similarly high average seed production (fig. 2*B*). When we included data from plants that did not have a complete set of replicates, all of the analyses described above yielded similar results.

Table 1

Three-Way ANOVA with Treatment (Four Levels), Year (Two Levels), and Color (Two Levels) as Main Factors and Seed Production per Fruit as the Dependent Variable

Source	df	*F*	*P*
Treatment	3	2.483	.060
Year	1	1.739	.188
Color	1	.503	.478
Treatment × year	3	5.864	.001
Treatment × color	3	.681	.564
Year × color	1	3.622	.058
Treatment × year × color	3	.279	.841
Error	480		

In the 2005 array experiment, plants with the control models were visited more frequently than plants with the other models (fig. 3*A*), and in the 2006 array experiment, model flowers within plants were visited with roughly equal frequency (fig. 3*B*). The heterogeneity *G*-tests showed that there was significant variation among replicate arrays in both years and that the distribution of visits significantly differed from the random expectation in 2005 but not in 2006 (table 2, null hypothesis A). When we restricted our comparison to the symmetric and asymmetric groups alone, there was some evidence to suggest that plants with symmetric flowers were visited more frequently than plants with asymmetric flowers ($P = 0.094$; table 2, null hypothesis B) but no evidence to suggest that symmetric flowers within a plant were visited more frequently than asymmetric flowers within a plant ($P = 0.277$; table 2, null hypothesis B).

Discussion

Combined, our results suggest that insect visitors to *Hesperis matronalis* do not use floral symmetry as a cue to make visitation decisions among plants and that they do not discriminate among flowers within plants on the basis of symmetry. In the first array experiment, which consisted of model plants that bore the same treatment on the entire plant, visitation frequencies to each of the treatment groups was significantly different from the random expectation. Plants with control flowers had a substantially higher visitation frequency than all other types. These plants had symmetric flowers and also the largest flowers; the symmetric and asymmetric flowers were 6.25% smaller than the control flowers, and the severely asymmetric flowers were 25% smaller than the control flowers. When the visitation frequency to plants with symmetric flowers was directly compared with the visitation frequency to plants with asymmetric flowers (equal floral areas but different symmetry), there was a trend suggesting that insects preferred to visit plants with symmetric flowers ($P = 0.094$). However, it should be noted that plants with the severely asymmetric treatment had a visitation frequency intermediate to those with symmetric and asymmetric flowers. The second array experiment consisted of model plants that each bore all four types of model flowers (and

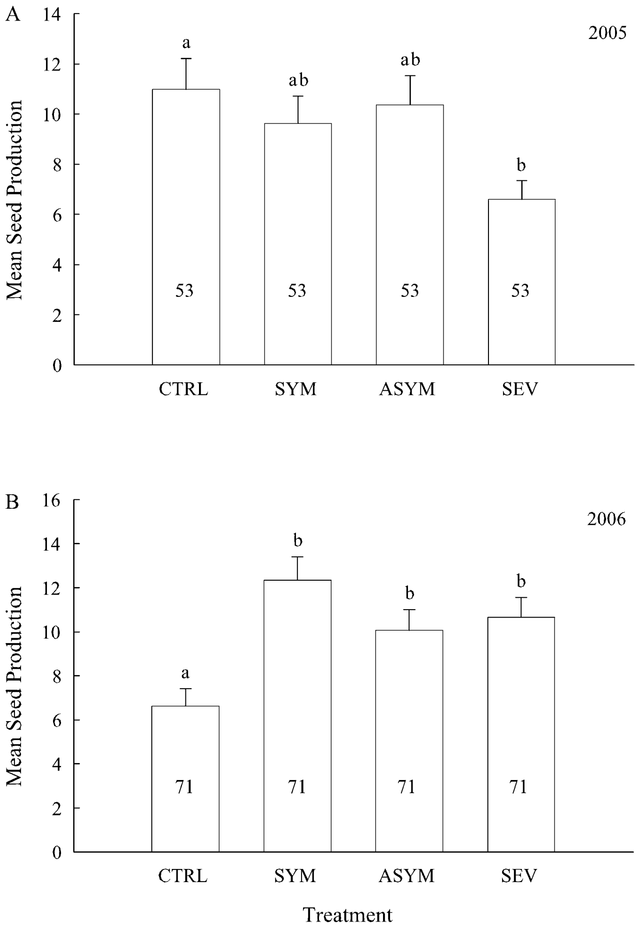

Fig. 2 Seed set per fruit (mean ± 1 SE) in each treatment group on plants that retained all four treatments in (*A*) 2005 ($n = 53$) and (*B*) 2006 ($n = 71$). The labels *CTRL*, *SYM*, *ASYM*, and *SEV* denote the control, symmetric, asymmetric, and severely asymmetric treatments, respectively. Treatment had a statistically significant effect on average seed production per fruit (2005: $F_{3,211} = 3.221$, $P = 0.024$; 2006: $F_{3,283} = 6.675$, $P < 0.001$). Letters denote homogeneous subsets identified through a post hoc Tukey analysis.

therefore plants had the same total floral area), and our results showed that visitation frequencies did not differ from the random expectation.

This design and these results are similar to our replicated manipulation experiment. In both years, we found no significant differences in seed production per fruit between the symmetric and asymmetric treatment groups. In 2005, flowers in the severely asymmetric treatment group had the lowest seed production, and this average value was significantly different from that of flowers in the control group. In 2006, however, flowers in the control group had the lowest seed production, and production values for flowers in the severely asymmetric treatment group were among the highest values. Although we cannot explain why flowers in the control group had lower seed production than expected in 2006, the results with respect to floral symmetry are clear. Manipulating floral symmetry while holding floral area constant in two concurrent years did not affect female reproductive success. These results could suggest that the pollinators of *H. matronalis* do not preferentially visit symmetric flowers over asymmetric flowers within or among plants. However, these results could also be explained if pollinators and pollen were not limiting in the population during the field study.

Previous studies that have used experimental arrays, floral manipulations, and direct estimates of the strength of pollinator-mediated selection have indicated that plants that produce large flowers are preferentially visited over plants that produce small flowers (Campbell 1989; Galen 1989; Young and Stanton 1990; Stanton et al. 1991; Møller and Sorci 1998), and our results are consistent with this work. In addition, several other studies have failed to find a link between floral symmetry and plant fitness. For example, Frey et al. (2005) manipulated floral symmetry in *Impatiens pallida* in two flowering seasons and found no association between symmetry and seed production. In addition, Malo et al. (2001) found limited effects of extreme floral mutilation on pollinia removal and fruit initiation in *Myrmecophila tibicinis*, and two studies

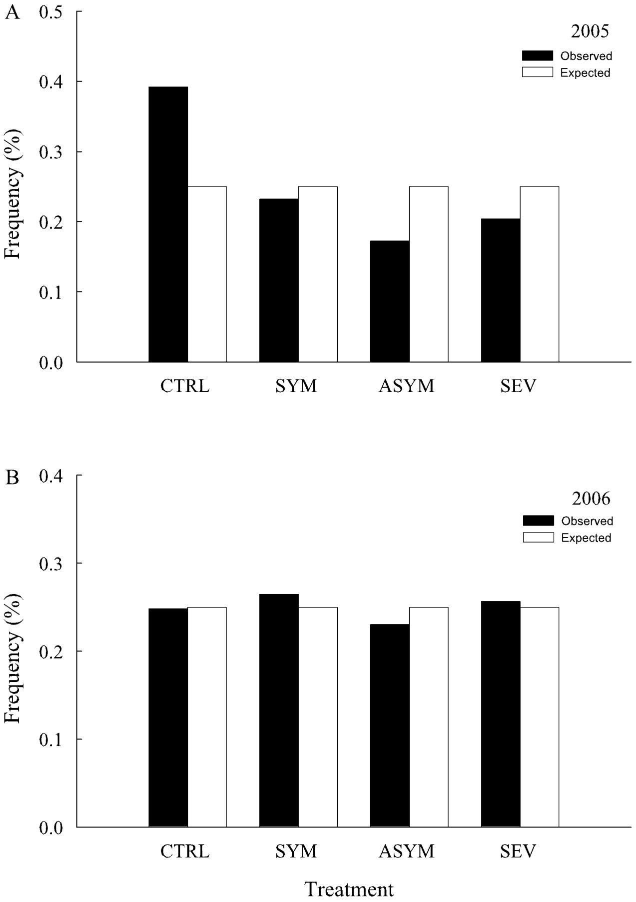

Fig. 3 Observed (filled bars) and expected (open bars) insect visitation frequencies to model treatment groups when treatments were distributed among plants (*A*, 2005) and within plants (*B*, 2006). The labels *CRTL*, *SYM*, *ASYM*, and *SEV* denote the control, symmetric, asymmetric, and severely asymmetric treatments, respectively. The observed distribution significantly differed from the expected distribution in 2005 ($G_{\text{pooled}} = 33.82$, $P < 0.001$) but not in 2006 ($G_{\text{pooled}} = 1.30$, $P = 0.729$).

Table 2

Heterogeneity *G*-Tests for Both Array Experiments

	2005			2006		
	df	*G*	*P*	df	*G*	*P*
Null hypothesis A:						
Pooled	3	33.82	< .001	3	1.30	.729
Heterogeneity	21	106.11	< .001	33	53.52	.013
Total	24	139.93	< .001	36	54.82	.023
Null hypothesis B:						
Pooled	1	2.81	.094	1	1.18	.277
Heterogeneity	7	18.72	.009	11	23.59	.015
Total	8	21.53	.006	12	24.77	.016

Note. Null hypothesis A = the distribution of visits to each of the four treatments was random. Null hypothesis B = the distribution of visits to the symmetric and asymmetric treatments alone was random.

that investigated the relationship between floral symmetry and pollinator behavior using model flowers also failed to find a clear link (Midgley and Johnson 1998; West and Laverty 1998). Conversely, several studies utilizing natural flowers and model flowers have shown that pollinators preferentially visit symmetric forms over asymmetric forms (Møller and Eriksson 1994, 1995; Lehrer et al. 1995; Møller 1995; Møller and Sorci 1998). It is difficult to compare the results of these studies because several different plant and pollinator systems were used in the manipulation experiments and because of the varied conditions under which the array experiments were performed. Studies assessing insect preferences for symmetry have been conducted under carefully controlled laboratory conditions (Lehrer et al. 1995) and in the field with real flowers or models that have had varying degrees of similarity to naturally occurring forms (Møller and Sorci 1998; West and Laverty 1998). Although there are these comparative difficulties, the contrasting results concerning direct manipulation of floral symmetry and female reproductive success could result from several factors. There are probably differences among species with respect to the number of pollinator visits necessary for full seed set, and these result in differences in the opportunity for selection on floral symmetry through female reproductive success (Frey et al. 2005). In addition, it is well known that bee pollinators can learn novel and complex visual tasks (Giurfa et al. 2001; Zhang et al. 2004; Dyer et al. 2005) and that these learning abilities are highly flexible given the proper training regime (Giurfa et al. 1999; Chittka et al. 2003). In situations where nectar resources are limiting, it is possible that innate preferences for symmetry might be replaced by learning whatever visual task is necessary to collect nectar.

In conclusion, our results add to the growing literature concerning the relationships between floral symmetry, pollinator preferences, and plant fitness. In this system, we find no compelling evidence to support the hypothesis that asymmetric flowers have lower seed production per fruit compared to symmetric flowers, that asymmetric flowers are visited less frequently than symmetric flowers, or that plants with asymmetric flowers receive less visitation than plants with symmetric flowers. Although we did not directly investigate whether floral symmetry is associated with male reproductive success, our combined results suggest that this is unlikely. Continued investigation in other species utilizing both field manipulation approaches and experimental arrays to assess patterns of insect visitation are necessary before any general conclusions can be made concerning the adaptive nature of floral symmetry.

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