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Evolution

Bumblebee preference for symmetrical flowers

(*Bombus terrestris/Epilobium angustifolium*/fluctuating asymmetry/nectar/pollination)

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ABSTRACT **Fluctuating asymmetry, which represents small random deviations from otherwise bilateral symmetry, is a measure of the phenotypic quality of individuals indicating the ability of controlled development under given environmental and genetic conditions. I tested whether floral symmetry reliably reflects phenotypic quality measured in terms of pollinator rewards and whether pollinators respond to floral symmetry in a series of observations and experiments on *Epilobium angustifolium* (Onagraceae). Lower petal asymmetry was negatively related to mean lower petal length, whereas asymmetry in leaf width was positively related to mean leaf width. Flowers visited by bumblebees were larger and more symmetrical than the nearest neighboring flower. This relationship between pollinator preference for large and symmetrical flowers was demonstrated to be causal in experiments in which the lower petals were manipulated symmetrically or asymmetrically. Nectar production was larger in symmetrical flowers, and this may explain the bumblebee preference for flower symmetry. Floral symmetry therefore reliably reflects nectar production and hence enhances pollen transport. Extensive embryo abortion has been documented in *E. angustifolium* and other outcrossing plant species. Floral fluctuating asymmetry, which reflects general developmental homeostasis, may explain such developmental selection in these plants.**

The evolution of floral characters may be viewed as the outcome of selection on floral traits by pollinators (e.g., refs. 1 and 2). Flowers are used in signaling between the plant and the pollinator, and pre-pollination selection of mates (before deposited pollen has started to grow) may depend on floral traits that manipulate pollinators in order to promote the receipt of preferred pollen or the export of pollen. Pollinator preferences should therefore result in strong directional selection for attractive flowers, and a number of studies have shown that pollinators preferentially visit flowers with the most extravagant floral traits (e.g., refs. 3–5). Pre-pollination selection may result in modified floral traits due to assortative mating between plants with attractive flowers. Flowers may be attractive to pollinators because they are either attractive arbitrary traits or reliable quality indicators in terms of pollinator rewards.

Pollination efficiency (measured as the efficiency with which plants attract pollinators and achieve fertilization) increases with the number of pollinators while pre-pollination selection may rely on pollinators that visit a particular subset of available flowers. These two processes can be antagonistic, because selection for greater pollination efficiency is positively frequency dependent. Selection for greater pollination efficiency should therefore result in stabilizing selection on floral traits if specialization on flowers of modal phenotypes by pollinators improves pollinator efficiency. Pre-pollination selection for large and extravagant flowers should have a strong directional component because only the largest and most extravagant phenotypes would be preferred by pollinators. Pollinator preferences for extreme floral phenotypes therefore cannot be explained by selection for increased pollination efficiency but have to be due to pre-pollination selection for attractive traits or reliable quality indicators.

Fluctuating asymmetry, which represents small random deviations from otherwise bilateral symmetry, is one measure of phenotypic quality that indicates the extent to which an individual has been able to control its development under given environmental and genetic conditions (6, 7). Asymmetry has also been described as an indicator of the ability of individual plants to cope with various kinds of stress (e.g., refs. 8 and 9). Asymmetry in floral traits is a potentially important determinant of pollinator visits (10, 11). Floral traits have the smallest degree of asymmetry in the largest flowers in a number of plant species, and this is directly opposite to the pattern for leaves, which tend to exhibit the largest degree of asymmetry in the largest leaves (11). These findings suggest that the size of flowers reliably reveals the phenotypic quality of plants because plant individuals with large and costly flowers are able to produce symmetrical flowers despite their large size.

The main aims of this study were (*i*) to test whether floral asymmetry is inversely related to the size of floral characters, (*ii*) to determine whether bumblebees prefer symmetrical flowers over asymmetrical ones, and (*iii*) to determine whether flower symmetry reliably reflects nectar production.

METHODS

I investigated floral fluctuating asymmetry and flower visits in a number of study plots around Kraghede (57°12′ N, 10°00′ E), Denmark, 10 June–30 August 1992 and 25 June–15 August 1993. Eight of the 10 sites were small coniferous plantations dominated by spruce *Picea abies*, while two other sites were peat bogs with shrub dominated by different species of willow *Salix* spp.

Epilobium angustifolium (Onagraceae) (Fig. 1) is a common perennial herb growing in woodlands and plantations in the study area. Ramets were 80–160 cm high and had one to three inflorescences with 80–120 flowers each (12). The bilaterally symmetric flowers are hermaphroditic and strongly protandrous. The male phase lasts ≈24 hr, during which the eight anthers open in sequence (13). The anthers deflex as most pollen has been removed, while the style moves forward during the female phase (13). While the flowers are genetically self-compatible (14, 15), self-pollination is prevented within the flowers due to the temporal dichogamy (13). The probability of geitogamy is apparently small because bumblebees move from basal, female-phase flowers toward the male-phase, pollen-carrying flowers (16, 17).

All flowers used for measurements and experiments had opened during the last 24 hr and were in male phase. Length of the two lower petals was measured as shown in Fig. 1. Petal asymmetry was determined as the unsigned difference in the length of the right and the left lower petal. Leaf asymmetry was

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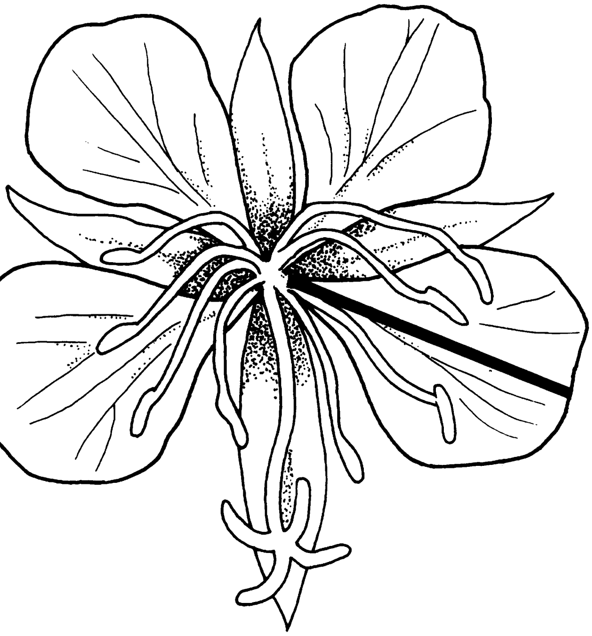

FIG. 1. Drawing of one flower from an inflorescence of *E. angustifolium*. The line indicates the length of the left lower petal.

determined as the unsigned difference in the width of the left and the right side of the leaf outside the mid-rib at the widest point. Character size (petal length, leaf width) was simply the mean of the left and the right character. I walked along transects through my study area and chose the first ramet encountered. I then chose the most recently fully developed flower and the leaf closest to the inflorescence for measurements. Withered or damaged flowers and leaves were excluded.

Characters demonstrating fluctuating asymmetry have normal frequency distributions of signed left-minus-right character values with a mean not deviating from zero (18). The petal trait did show fluctuating asymmetry as demonstrated by the average signed left-minus-right differences not deviating significantly from zero [one-sample t test: $t = 0.04$, df = 199, not significant (NS)] and the differences not deviating from a normal distribution (Kolmogorov–Smirnov test, $D = 0.06$, NS). Absolute asymmetry was estimated as the unsigned left-minus-right character value (18).

Measurement errors were estimated by measuring petals and leaves of 10 flowers and 10 leaves and then remeasuring exactly the same flowers and leaves again. The repeatabilities (R; ref. 18) were for petal length $R = 0.99$, SE = 0.01, $F = 3339.54$, df = 9, 10, $P < 0.001$, and for absolute petal asymmetry $R = 0.95$, SE = 0.03, $F = 42.23$, df = 9, 10, $P < 0.001$. The consistency of length and asymmetry of lower petals and leaves was estimated by measuring two flowers and two leaves on 200 ramets and analyzing the repeatability of the traits (19).

I tested for preferences for symmetrical flowers by locating the first flower on a ramet visited by the bumblebee *Bombus terrestris* during a total of 50 hr of observations. Each single observation thus consisted of an observation of a bumblebee on a random flower. The length of the two lower petals was then measured for this visited flower and the nearest neighboring flower on the same ramet that was not visited by the bumblebee. The insect had a clear possibility to choose between these two flowers because the distance was very short. Differences in lower petal length and lower petal asymmetry were smaller within than among ramets (22% of the variance occurred within ramets and 78% among ramets; see *Results*), and this may make discrimination more difficult.

I tested for assortative visits to symmetrical flowers by determining the degree of fluctuating asymmetry in petal length of a flower in male phase visited by a bumblebee and the degree of asymmetry of the nearest neighboring flower on the same ramet during a total of 31 hr of observations. Similar measurements were made for the flower on the subsequently visited ramet and its nearest neighboring flower on the same ramet. Visits are assortative when there is an excess of visits to symmetrical flowers and asymmetrical flowers on subsequently visited ramets. Individual flowers visited by bumblebees were classified as being more or less asymmetric than the nearest neighboring flower and the subsequent flower visited by the bumblebee as being more or less asymmetric than the new, nearest neighboring flower. The data were analyzed in a 2 × 2 contingency table with two symmetric cells for one flower being more asymmetric than the nearest neighbor and the other being less asymmetric than the nearest neighbor (20). Observed and expected values were thus calculated for the two cells with assortative visitation for more and less symmetry than the nearest neighboring flower.

I estimated nectar production by bagging inflorescences with fine mesh tied close to the stalk 1 week before the start of flowering, and this prevented pollinators from access to the nectar. Bagging of inflorescences may have affected nectar production (21), although this effect is unlikely to have affected the ranking of ramets with respect to nectar production. A single fully developed flower in male phase [which lasts 24 hr (12)] was located on bagged ramets 2 days following opening of the first flower, and fluctuating asymmetry in lower petal length of this flower was estimated as the unsigned difference in length between the two lower petals. The nectar content of the same flower was measured with a 5-μl microcapillary tube. Nectar production during 48 hr was thus measured at the beginning of the flowering period of each ramet and in most cases during the first half of the flowering period of all ramets in the population.

Lower petal asymmetry and lower petal size were experimentally manipulated in an attempt to determine whether bumblebees demonstrate any preference for symmetrical and large flowers. One fully developed flower in the apical-most position on each of four different, neighboring ramets with a maximum inter-ramet distance of 30 cm was randomly assigned to one of four treatments. The number of opened flowers differed among ramets, but this should not be important because of random assignment of treatments. The first treatment consisted of cutting 2.0 mm from a randomly chosen lower petal with a pair of scissors maintaining the shape of the petal (asymmetric). This reduced mean lower petal length by 7% to 13.1 mm and increased mean lower petal asymmetry to 2.5 mm. The second treatment consisted of cutting 1.0 mm from both of the two lower petals with a pair of scissors maintaining the shape of the petals (symmetric II). This resulted in a reduced mean lower petal length by 7% to 13.2 mm but did not increase lower petal asymmetry, which on average was 0.5 mm. The third treatment consisted of cutting 2.0 mm from both of the two lower petals with a pair of scissors maintaining the shape of the petals (symmetric I). This reduced mean lower petal length by 14% to 12.1 mm but did not affect lower petal asymmetry, which on average was 0.5 mm. The final group was a control group in which lower petals were handled but remained uncut. Mean lower petal length was 14.2 mm and mean lower petal asymmetry was 0.4 mm in this group. A quadruplet with these four treatments was considered one replicate. The first of the four flowers in a replicate visited by a bumblebee was recorded and then a new replicate was initiated. A total of 20 replicates were made in each of 10 experiments, yielding a total of 200 replicates. A total of 80 ramets was therefore involved in experiments in each site, in total 800 ramets in the 10 sites.

Values reported are means (±SE).

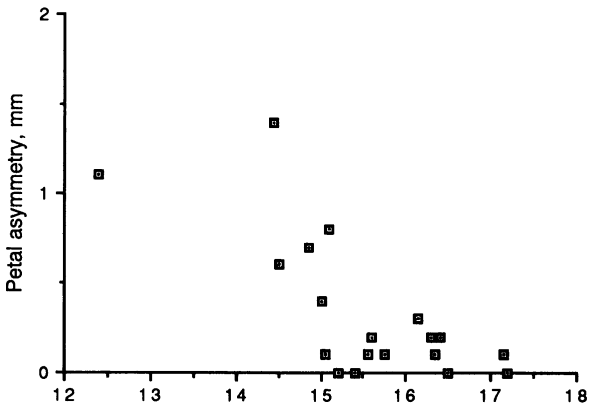

FIG. 2. Relationship between lower petal asymmetry and lower petal length in one sample of 20 flowers each from a different ramet of *E. angustifolium*. The relationship is statistically significant and negative ($F = 17.13$, df = 1, 18, $P = 0.0006$). Two data points overlap at 16.5-mm petal length and 0-mm petal asymmetry.

RESULTS

There was a negative relationship between the degree of fluctuating asymmetry in lower petal length and lower petal length in the flowers of *E. angustifolium* (one example of this negative relationship for one sample of 20 flowers each from a different ramet is shown in Fig. 2). The mean of the 10 standardized regression coefficients for this relationship in 10 different samples of 20 ramets each was on average −0.25 (0.06), range −0.06 to −0.69, differing significantly from zero (one-sample t test: $t = 4.11$, df = 9, $P = 0.003$). There was also a negative relationship between petal asymmetry and petal length when using mean values for the samples as independent data points [$F = 464.93$, df = 1, 8, $r^2 = 0.98$, $P < 0.001$; mean petal asymmetry (mm) = 9.59 − 0.57 (0.03) mean petal length (mm)]. Large flowers therefore exhibited less fluctuating asymmetry in lower petal length than did small flowers.

The relationship between leaf asymmetry and leaf size was positive with an average standardized regression coefficient of +0.16 (0.04), range 0.01–0.33, in 10 different samples of 20 ramets each, differing significantly from zero (one-sample t test: $t = 4.59$, df = 9, $P = 0.001$). Leaf asymmetry and leaf size were positively correlated when using mean values for the samples as independent data points [$F = 157.84$, df = 1, 8, $r^2 = 0.95$, $P < 0.001$; mean leaf asymmetry (mm) = 0.046 + 0.088 (0.007) mean leaf width (mm)]. The pattern of asymmetry for lower petals was therefore different from that of leaves, which play no role in pollination.

If characteristics of floral traits were reliable indicators of phenotypic quality, one should expect that different flowers on the same ramet would demonstrate consistency in the expression of floral characters. This was in fact the case since the consistency of lower petal length and degree of fluctuating asymmetry in the length of lower petals among flowers on the same ramet was statistically significant [lower petal length: $R = 0.83$ (0.02), $F = 10.56$, df = 191, 192, $P < 0.0001$; lower petal asymmetry: $R = 0.22$ (0.10), $F = 1.29$, df = 191, 192, $P < 0.01$]. The consistency of floral asymmetry was considerably smaller than that of petal size.

The degree of lower petal asymmetry in flowers visited by a bumblebee was smaller than that of the nearest neighboring flower on the same ramet that was ignored by the visitor [10 different samples of 20 ramets each (mean of the mean asymmetry of each sample): flowers visited first by a bumblebee: 0.39 mm (0.07); flowers not visited first: 0.60 mm (0.11), paired t test, $t = 5.54$, df = 9, $P = 0.0004$]. First-visited flowers were also larger than the nearest neighboring flower not visited first by a bumblebee [(mean of the mean length of each sample): flowers visited first: 16.0 mm (0.11); flowers not visited first: 13.9 mm (0.07), paired t test, $t = 5.48$, df = 9, $P = 0.0005$)]. There were independent effects of lower petal size and lower petal asymmetry on first visits by bumblebees as determined from a partial correlation analysis. Large and symmetric flowers were visited first more often than small and asymmetric flowers (lower petal length: Kendall $\tau = 0.153$, $n = 200$, $z = 3.10$, $P = 0.002$; lower petal asymmetry: Kendall $\tau = -0.150$, $n = 200$, $z = 3.04$, $P = 0.002$). Bumblebees thus appeared to pay attention to both features of flower morphology.

There was an excess of bumblebee visits to more symmetrical flowers and a deficit of visits to less symmetrical flowers (Table 1). This difference was statistically significant ($G^2 = 48.24$, df = 1, $P < 0.001$). Preferential bumblebee visits to symmetrical flowers resulted in assortative visits with respect to fluctuating asymmetry in floral traits as shown by the excess of visits to pairs of flowers that were less asymmetric than the nearest neighboring flower (observed: 88, expected: 80.9, $G^2 = 7.40$, df = 1, $P < 0.01$). More important, there was also an excess of visits to pairs of flowers that were more asymmetric than the nearest neighboring flower (observed: 19, expected: 11.9, $G^2 = 8.89$, df = 1, $P < 0.01$). The prediction that preferential pollinator visits to symmetrical flowers resulted in assortative visitation with respect to fluctuating asymmetry in petal length was therefore fulfilled.

I tested whether bumblebee visits to flowers were determined by the degree of petal asymmetry by experimentally manipulating asymmetry and size of the two lower petals. Mean length of lower petals differed among groups after the treatment ($F = 14.09$, df = 3, 196, $P < 0.001$) but did not do so before the treatment ($F = 0.42$, df = 3, 196, NS). The mean degree of absolute asymmetry of lower petals differed among groups after the treatment ($F = 115.22$, df = 3, 196, $P < 0.001$) but did not do so before the treatment ($F = 0.37$, df = 3, 196, NS). There was a clear difference in pollinator visitation rates to flowers belonging to the different treatments (Fig. 3). First visits were made to asymmetric flowers least often, then symmetric I flowers, symmetric II flowers, and most often to control flowers. Symmetric flowers were preferred over asymmetric ones since the symmetric II flowers were chosen first more often than the asymmetric flowers. There is also an effect of flower size on pollinator visits since symmetric II flowers were chosen first more often than symmetric I flowers and since control flowers were visited first more often than symmetric II flowers. Alternatively, bumblebees may have responded to relative petal asymmetry, since relative asym-

Table 1. Assortative bumblebee visits with respect to petal asymmetry

	First flower less asymmetric than nearest neighbor	First flower more asymmetric than nearest neighbor	Total
Second flower less asymmetric than nearest neighbor	88	26	114
Second flower more asymmetric than nearest neighbor	22	19	41
Total	110	45	155

Numbers are numbers of pairs of flowers on two ramets visited by *B. terrestris*.

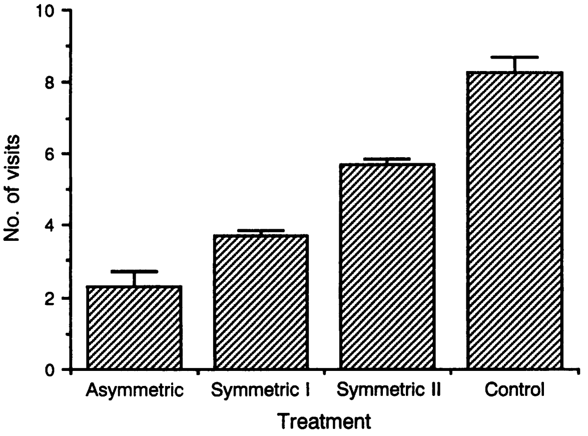

FIG. 3. First bumblebee visits to flowers of *E. angustifolium* in relation to experimental treatments of the lower petals. Values are the mean number of flowers (+1 SE) visited in 10 experiments each with 20 replicates. There was a statistically significant difference in first visits to flowers receiving the four different treatments ($F = 71.02$, df = 3, 36, $P < 0.0001$). Differences among treatments were all statistically significant ($P < 0.05$, Scheffe F tests).

metry decreased from symmetric I flowers over symmetric II flowers to control flowers. These experiments demonstrate that bumblebees use petal symmetry and perhaps petal size as cues in their choice of flowers.

Nectar production of flowers was negatively related to asymmetry of lower petals (one sample of 20 flowers each from a different ramet is shown in Fig. 4). Multiple regression revealed that the mean standardized regression coefficient for 10 different samples (clones) of 20 ramets each was −0.19 (0.02), range −0.12 to −0.31, for lower petal asymmetry, and +0.31 (0.11), range 0.01–0.67, for lower petal length. Both mean values are significantly different from zero (one-sample *t* test: lower petal asymmetry: $t = 9.70$, df = 9, $P < 0.0001$; lower petal length: $t = 2.90$, df = 9, $P = 0.018$). There were also significant relationships between nectar content and petal asymmetry and petal length, respectively, when using mean values for the samples as independent data points [multiple regression: $F = 1011.36$, df = 2, 7, $r^2 = 0.98$, $P < 0.001$; mean nectar production (μl) = −3.16 − 0.50 (0.15; $P < 0.01$) mean petal asymmetry (mm) +0.23 (0.09; $P < 0.05$) mean petal length (mm)].

DISCUSSION

This paper tests two hypotheses: (*i*) that floral symmetry reliably reflects phenotypic quality of plants in terms of the size of pollinator rewards and (*ii*) that pollinators use floral symmetry in their choice of flowers, apparently because symmetrical flowers provide larger pollinator rewards. The negative relationship between petal asymmetry and petal size is consistent with the view that plant individuals with larger flowers are of higher phenotypic quality than plants with smaller flowers (11, 22). This pattern differs from the null expectation of no relationship between asymmetry and character size commonly found in morphological characters in animals (22–24). The relationship between asymmetry and size of petals was opposite to that for leaves, which demonstrated increasing asymmetry with increasing leaf size, in accordance with previously reported results for a number of other plant species (11).

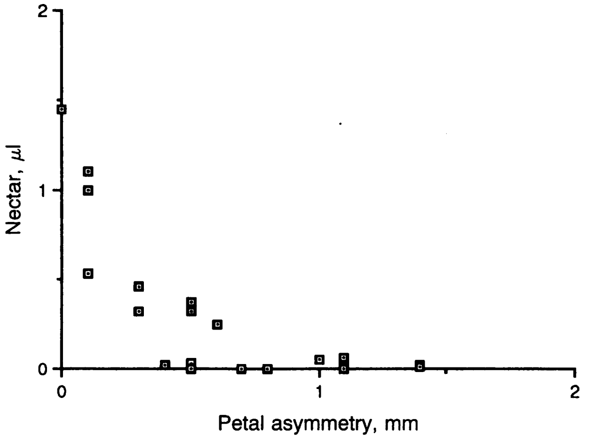

FIG. 4. Relationship between nectar content and lower petal asymmetry in one sample of 20 flowers each from a different ramet of *E. angustifolium*. The relationship is statistically significant and negative ($F = 20.45$, df = 1, 18, $P = 0.0003$).

The observations and the petal-cutting experiments revealed that bumblebees preferred symmetrical and perhaps large flowers over small and asymmetrical ones. The preference for symmetrical flowers could either be mediated through a low nectar production being associated with petal asymmetry, asymmetrical nectar guides being associated with petal asymmetry, or both. Bumblebees visited flowers assortatively, since there was an excess of visits to pairs of flowers that were less asymmetric and more asymmetric than the nearest neighboring flowers (Table 1). High first visitation rates to large flowers verify previous reports of the importance of flower size for pollinator attraction (3–5). The hypothesis that pollinators prefer large flowers has previously been tested by experimental removal of petals (3), a result interpreted as suggesting that pollinators prefer large flowers. However, the manipulation simultaneously altered flower size and symmetry, and the lower visitation rate to manipulated flowers could be caused by either of these factors affecting pollinator visits. The petal-cutting experiment on *E. angustifolium* clearly demonstrated that petal asymmetry and perhaps petal size were important determinants of visits.

The association between flower asymmetry and first bumblebee visitation rates of *E. angustifolium* may indicate that there are fitness benefits associated with floral symmetry. (*i*) The preference for large, symmetrical flowers may give rise to higher visitation rates, which may result in more pollen being exported (or at least more pollen being removed from the anthers) and more pollen being received by preferred flowers. Higher pollen acquisition by flowers may increase seed production or the quality of offspring. (*ii*) The preference for large, symmetrical flowers may result in assortative mating between ramets that grow under relatively good conditions or are of high genotypic quality. Pollen exported from large, symmetrical flowers may therefore produce more or higher quality offspring, and large, symmetrical flowers may receive pollen of higher quality. (*iii*) There may be a direct coupling between extensive embryo abortion in *E. angustifolium* during early stages of cell differentiation (15) and developmental homeostasis in flowers as reflected by fluctuating asymmetry in floral traits. Wiens *et al.* (15) interpreted a seed to ovule ratio of 0.37 in their study of *E. angustifolium* as indicating developmental selection due to genetic load in a highly outcrossing species. Early embryo death is the consequence of serious developmental failures (15), and developmental failure during floral morphogenesis is the process resulting in floral asymmetry. It is thus possible that levels of embryo abortion will be linked directly to levels of floral asymmetry in parents, because both processes are the outcome of the same general system of developmental control.

I studied the relationships among floral size and symmetry, nectar production, and bumblebee visitation at the within-clone and the among-clone levels. Clones of *E. angustifolium* were distinguished from each other by the presence of old roads or open fields separating groups of ramets. There was statistically significant covariation among these traits within clones and among floral size and symmetry and nectar production among clones. Within-clone variation may only give rise to relatively small fitness benefits, if there is competition for pollinator service among ramets within a clone. If competition for pollination within a clone is won by ramets that grow under relatively favorable conditions and thus produce large and symmetrical flowers with high nectar contents, this may be beneficial to the clone because these ramets have the highest potential reproductive output. However, if there are even slight genetic differences among ramets within a clone, this will give rise to attempts by ramets to produce as large and symmetrical flowers as possible in order to win at competition for pollinator services.

If we assume that symmetrical flowers give rise to fitness benefits for the ramet, why do not all ramets produce large and symmetrical flowers? If flowers are subject to a recent history of net directional selection for altered morphology, as evidenced from larger divergence in floral as compared to foliar traits among closely related species (e.g., species belonging to the genus *Epilobium*), this will result in an increased level of fluctuating asymmetry, and only plants of a specific genetic constitution may be able to maintain flower symmetry (22). Asymmetric phenotypes will be produced continuously due to the directional selection pressure, and mutations may continuously give rise to disruption of developmental stability and thus production of asymmetrical flowers. This means that some individuals always are unable to develop symmetrical phenotypes under current environmental conditions.

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