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Insect preference for symmetrical artificial flowers

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Abstract An insect preference for floral symmetry may be maintained because plants with symmetrical flowers, which are able to control developmental processes under given environmental conditions, also are able to provide more pollinator rewards than plants with asymmetrical flowers. Alternatively, insects may have an inherent preference for symmetrical structures and thereby impose selection for the maintenance of symmetry in flowers even in the absence of any pollinator rewards. We tested for an insect preference for radially symmetrical flowers by using horizontally placed units of four circular coloured flower models varying in size and symmetry. The shape and colour of the model flowers did not resemble any naturally occurring flowers in the environment. Insects and Hymenoptera, respectively (five species of Diptera and one species of Coleoptera) that visited the flower models clearly preferred symmetrical models over asymmetrical ones, and the ranking of visits to the models reflected a preference for large, symmetrical flowers. These results provide evidence for a preference for symmetrical flower models, even in the absence of pollinator rewards.

Key words Developmental stability · Fluctuating asymmetry · Plant sexual selection · Pollinator rewards

Introduction

Flowers generally display striking bilateral or radial patterns of symmetry in morphology and coloration. This apparent regularity of phenotypes hides considerable amounts of irregularity. For example, the average level of relative radial or bilateral asymmetry in flowers

of 19 species of plants ranged from 1.5% to 14.9% of the size of flowers, with considerable intraspecific variation (Møller and Eriksson 1994). Some variation in asymmetry has a genetic basis (Møller and Thornhill 1997; Møller and Swaddle 1997), and asymmetrical and irregular phenotypes might therefore spread unless controlled by natural or sexual selection. Symmetrical phenotypes may be maintained by selection because symmetrical individuals perform better than asymmetrical ones.

Phenotypic traits of plants and other organisms demonstrate small, randomly directed deviations from symmetrical phenotypes termed fluctuating asymmetries. Such deviations reflect the ability of the individual to control developmental processes under given environmental conditions, and fluctuating asymmetry therefore provides a direct measure of developmental instability (e.g. Ludwig 1932; Parsons 1990; Møller and Swaddle 1997). A large number of genetic and environmental factors are known to affect asymmetry and alternative measures of developmental instability in plants (Mather 1946; Paxman 1956; Huether 1968, 1969; Bagchi and Iyama 1983; Bagchi et al. 1989; Ellstrand 1983; Martin and Sutherland 1990; Freeman et al. 1993; Møller 1995a, b, 1996; Evans and Marshall 1996; Sherry and Lord 1996a, b; Møller and Swaddle 1997). Environmental factors include nutrients, pathogens, intra- and interspecific competition, and radiation, while genetic factors include mutation, hybridisation, inbreeding, and sometimes homozygosity. Deviations from a perfectly symmetrical phenotype thus provide a measure of the ability of an individual to cope with its environment given its genetic background.

Developmental instability as assessed from fluctuating asymmetry has recently been suggested to be a cue used by two species of pollinators (bumblebees *Bombus terrestris* and honey bees *Apis mellifera*) in their choice of flowers, independent of whether this was based on natural variation in asymmetry or experimentally manipulated asymmetry (Horridge and Zhang 1995; Møller and Eriksson 1995; Møller 1995a; Eriksson 1996; Giurfa et al. 1996). Previous studies of pollinator preferences

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for flowers have indicated that large flowers are preferred over small flowers (Knoll 1922; Kugler 1943; Bell 1985; Stanton and Preston 1988; Campbell 1989; Galen 1989; Young and Stanton 1990). However, since flower size and asymmetry sometimes are negatively correlated (Møller and Eriksson 1994; Møller 1995a), and since experimental manipulation of flower size sometimes cannot be discriminated from manipulation of flower asymmetry (e.g. Bell 1985), an apparent preference for large flowers may just as well be interpreted as a preference for floral symmetry. Since symmetrical flowers of several species of plants, after controlling for any effects of flower size, have been found to produce more nectar, (Møller 1995a; Eriksson 1996) and have larger standing crops of nectar (Møller and Eriksson 1995), and nectar with higher sugar content (J.T. Manning, personal communication), pollinators are rewarded by visiting symmetrical rather than asymmetrical flowers. The positive association between floral symmetry and quality and quantity of pollinator rewards may arise because plant individuals of superior phenotypic and/or genetic quality have a superior ability to produce both a stable phenotype and large amounts of pollinator rewards. Such positive relationships between measures of individual developmental stability and performance in a number of different fitness domains have been reported repeatedly in a number of different plants and animals (review in Møller and Swaddle 1997).

Flower-visiting insects are known to use a wide range of cues in their choice of flowers such as size, colour, pollinator rewards, and ultraviolet reflectance of flowers (Waser and Price 1981; Menzel and Backhaus 1991; Willson 1991; Chittka and Menzel 1992; Dafni 1992; Kearns and Inouye 1993). A large number of potential cues are therefore available, and the relative importance of different cues is difficult to tease apart without experimental manipulations.

The main aims of the present study were to test for insect preferences for radially symmetrical flowerlike models in the absence of any confounding variables such as pollinator rewards, coloration and odours. This was done by presenting coloured paper models of flowers differing in their size and degree of radial asymmetry. By systematically varying the size and asymmetry of flower models, we were able to discriminate between insect preferences for size and symmetry.

Materials and methods

The experiments were carried out at Guadix (37°18'N, 3°11'W), Spain, during early April 1996, and at Kraghede (57°12'N, 10°00'E), Denmark, during June-July 1996. The study site at Guadix is a high-altitude plateau with extensive farming. The sites used for the experiments were uncultivated areas bordering fields. The most abundant flowering plants in this area were *Hypocoum imberbe*, *Eruca vesicaria*, *Lamium amplexicaule*, *Geranium rotundifolium*, *Prunus dulcis*, and *Tanacetum radicans*, which have bilaterally or radially symmetrical flowers. The flowers of these plants were visited by a wide variety of Lepidoptera, Diptera, Hymenoptera, and Coleoptera. The study site at Kraghede is an in-

tensely cultivated farmland area, and experiments were performed in field boundaries. The most common flowering plants in these areas were *Epilobium angustifolium*, *Valeriana officinalis*, *Knautia arvensis*, *Ranunculus arvensis*, *Potentilla reptans*, and *Brassica napus*, which have bilaterally or radially symmetrical flowers. Flower-visiting insects included many different species of Lepidoptera, Diptera, Hymenoptera, and Coleoptera. A total of 28 days amounting to more than 100 h of field observations between 0900 and 1800 hours were used for the experiments. The experimental set-up consisted of four paper models of flowers placed in a quadrat with sides of c. 15 cm. All paper flowers had a circular shape, but differed in diameter (18 mm, 24 mm, and 30 mm, respectively). Each of these three flower models had a black dot in the centre. The fourth model had a similar diameter to the intermediate-sized flower (24 mm), but the black dot was located so the minimum radius equalled the radius of the smallest model flower (9 mm), and the maximum radius equalled the radius of the largest model flower (15 mm) (Fig. 1). This level of asymmetry is within the range of naturally occurring asymmetries in the length of petals in a variety of plant species (Møller and Eriksson 1994). Therefore, the experimental design consisted of three symmetrical flowers of different size (Control, 30 mm diameter, Symmetric I, 24 mm diameter, Symmetric II, 18 mm diameter) and one asymmetrical flower (Asymmetric, 24 mm diameter, but with the black dot placed eccentrically). Each set of four flower models was attached with pins to a piece of cardboard in a quadrangle at a distance of c. 5 cm between circles, and each set of models was placed at ground level. Since insects differ in colour vision, we performed two series of experiments with yellow and red flower models, respectively. Yellow and red models were exposed to insects a similar amount of time.

A total of 260 of these units of four model flowers were placed horizontally on the ground in the field (80 at Guadix and 180 at Kraghede), where natural flowers were present. Units of models were put out in sunny weather when insects were abundant. The distance between units of models was 30–40 cm with a total of four to six units placed within an area. We made sure that the flower models did not mimic any of the natural flowers in either shape or colour. We captured all insects that landed on a model (defined as a visit) in order to avoid the possibility that a given insect individual visited the same flower model more than once. When we failed to capture an insect, we moved our experimental set-up several meters. We also systematically replaced each flower model visited, since insects might deposit pheromones on models and thereby induce other insects to visit or avoid the same model.

We used a *G*-test (Sokal and Rohlf 1981) to test the null hypothesis that the observed distribution of visits was random with an equal number of visits to each of the four experimental flower models. The predicted order of visits to the four kinds of models following the alternative hypothesis was Control > Symmetric I > Symmetric II > Asymmetric if insects preferred large structures over small ones (Symmetric I > Symmetric II), and if they preferred symmetrical over asymmetrical ones (Symmetric I and II > Asymmetric). If insects used the largest radius for assessment of flowers, they would visit Symmetric I and Asymmetric models equally often. If they used the smallest radius for assessment, they would visit Symmetric II and Asymmetric models equally often. If asymmetry was avoided compared to symmetry, this should result in the Asymmetric models being visited less often than any other models.

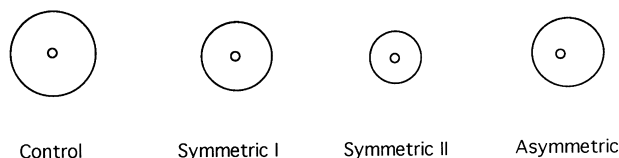


Fig. 1 Design of flower models used in the experiments. The diameters of the models were 30 mm (Control), 24 mm (Symmetric I), 18 mm (Symmetric II), and 24 mm (Asymmetric)

Table 1 Absolute abundance of insects visiting flower models

	Model color	Flower model			
		Control	Symmetric I	Symmetric II	Asymmetric
<i>Guadix</i>	Red				
Diptera		25	12	9	7
Hymenoptera		2		1	
Coleoptera		1		1	
Heteroptera		1	1		
	Yellow				
Diptera		9	6	3	2
<i>Kraghede</i>	Red				
Diptera		26	16	7	4
Hymenoptera		2	2	3	
	Yellow				
Diptera		18	15	15	2
Hymenoptera		4	4		1
Coleoptera		36	12	8	4
Lepidoptera				1	

Results

Most insects visiting our experimental flower models were Diptera and Hymenoptera in Guadix and Diptera, and Coleoptera and Hymenoptera in Kraghede, and these insects were also found commonly on real flowers in our study sites (Table 1). Three species of Diptera (*Cyclorrhapha*, *Schizophora*) dominated the samples from Guadix (87.5% of 80 insects captured) and two species of Diptera (*Cyclorrhapha*, *Schizophora*, mainly Muscidae and Syrphidae) and one species of Coleoptera (*Meligethes*) the samples from Kraghede (88.9% of 180 insects captured). Insects that visited real flowers often moved directly to one of the flower models, or approached from further away. There was no significant difference in the distribution of insects on red and yellow models (Guadix: Fisher exact test, $P = 0.92$; Kraghede: Fisher exact test, $P = 0.86$), and the data from the two types of experiments were therefore combined. The pattern of insect visits was similar in the two sites ($G = 2.10$, $df = 3$, $P = 0.74$). The observed distribution of insect visits was significantly different from random (Guadix: $G = 22.39$, $df = 3$, $P < 0.001$; Kraghede: $G = 69.69$, $df = 3$, $P < 0.001$). There was a clear preference for control flowers, which were the largest symmetrical ones, while asymmetrical flowers had the smallest number of visits (Fig. 2). Symmetrical I and II models received an intermediate number of insect visits. The observed distribution of insect visits on the four types of models differed significantly from a random expectation for Diptera (Guadix: $G = 19.02$, $df = 3$, $P < 0.001$; Kraghede: $G = 34.24$, $df = 3$, $P < 0.001$) and Coleoptera at Kraghede ($G = 40.59$, $df = 3$, $P < 0.001$).

Since the flower models of the Symmetric I and the Asymmetric treatments were of similar size, but differed

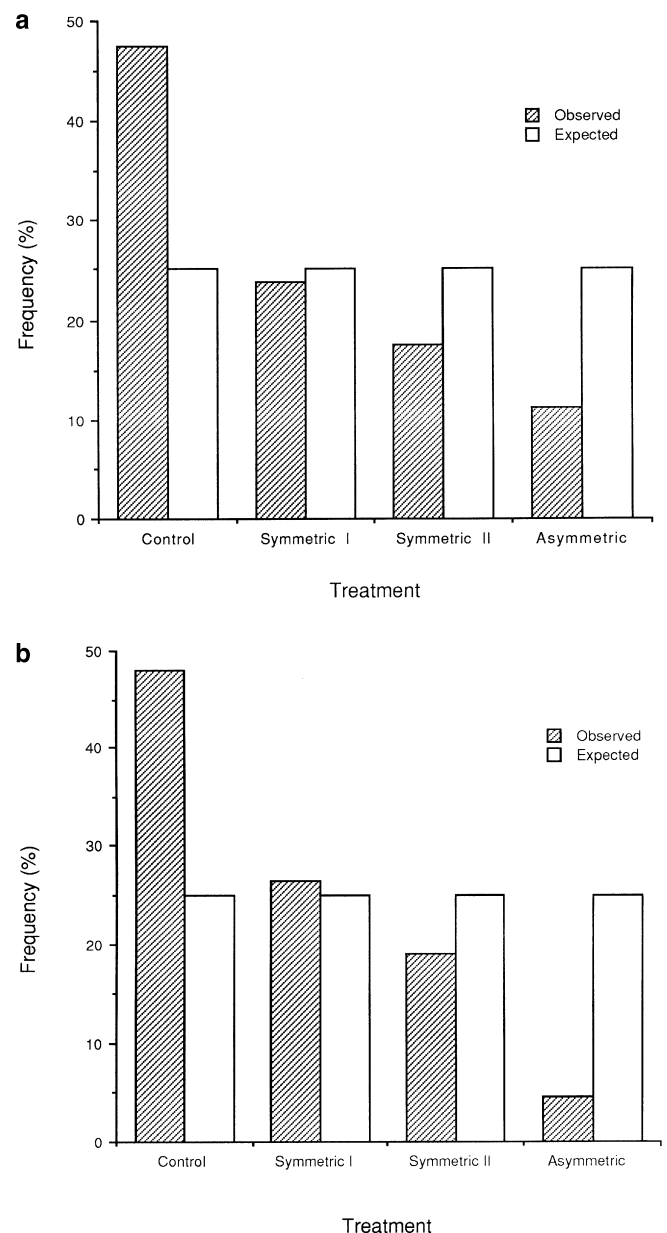


Fig. 2 Flower model preference for insects in the two experiments at **a** Guadix and **b** Kraghede. The numbers of insects in the experiments were 80 and 180, respectively, in the two trials

in asymmetry, we predicted from our null hypothesis of only size being important that insects therefore should be distributed evenly between these two types of models. The observed distribution of insects differed significantly from expectation in Kraghede (49 insects at Symmetric I versus 11 Asymmetric: $G = 26.01$, $df = 1$, $P < 0.001$), whereas the difference approached significance in Guadix (19 Symmetric I versus 9 Asymmetric: $G = 3.65$, $df = 1$, $P = 0.057$). The combined probability using Fisher's method was highly significant ($\chi^2 = 24.15$, $df = 4$, $P < 0.001$). The observed distribution of Diptera also differed significantly from expectation (Guadix: $G = 16.00$, $df = 1$, $P < 0.001$; Kraghede: $G = 3.86$, $df = 1$, $P < 0.05$), as did the distribution of Hymenoptera at Kraghede ($G = 3.96$, $df = 1$, $P < 0.05$) and Coleoptera at Kraghede ($G = 4.19$, $df = 1$, $P = 0.05$). Therefore, insects clearly preferred symmetrical models over the asymmetrical ones of the same overall size.

There was also good agreement between the predicted order of insect preferences for size and symmetry of flower models from the alternative hypothesis and the order observed. Given that the four models might have been ranked in 24 different ways, the probability of observing the predicted order by chance alone was for both the experiments 0.042. The combined probability from the two independent experiments is less than 0.015 ($\chi^2 = 12.68$, $df = 4$) using Fisher's method of combining probabilities.

Discussion

The experiments demonstrated that there was a preference by insects for symmetrical flower models over asymmetrical ones (Fig. 2; Table 1). This was the case even in the absence of any pollinator rewards and any variation in visual or olfactory cues. These results were similar for a range of different insect taxa (Table 1) suggesting that a wide variety of flower-visiting insects (Diptera, Coleoptera; Hymenoptera (Horridge and Zhang 1995; Møller 1995a; Giurfa et al. 1996)) might impose similar selection pressures on flower symmetry.

Why should insects prefer symmetrical flowers over asymmetrical ones? A number of possible answers include (1) a preference for flowers with more pollinator rewards, (2) a preference for symmetrical characters that exists for other reasons, (3) a pre-existing bias for symmetrical structures caused by the way in which the neural system is arranged, and (4) the insects did not recognize the asymmetrical models as flowers.

Pollination reward

Symmetrical flowers of several plant species, after controlling for the effects of flower size, have been shown to produce more nectar than asymmetrical flowers (Møller 1995a; Eriksson 1996), but also to have a larger standing

crop of nectar (Møller and Eriksson 1995) with a higher sugar content (J.T. Manning, personal communication). Insects that prefer symmetrical flowers over asymmetrical ones will benefit in terms of resource gain from their foraging. Since the flower models used in the present experiment did not mimic any naturally occurring flowers with respect to shape or colour, insects should only be able to use symmetry in their choice of flower models if they were able to categorize stimuli in terms of symmetry. Since all the insects captured in the experiment probably already had experience with real flowers, they may have learnt that symmetrical floral phenotypes provide a large amount of high quality pollinator rewards. An ability to categorize symmetry has been shown both for vertebrates (Rensch 1958; Delius and Habers 1978; Delius and Nowak 1982) and insects, even for naive ones (Horridge and Zhang 1995; Giurfa et al. 1996). Laboratory studies on honey bees have demonstrated that bees are readily trained to discriminate between flower models differing in degree of asymmetry (Horridge and Zhang 1995).

Preference for symmetry

The preference for symmetrical flower models may exist because there is a general preference for symmetry in other contexts. For example, preferences exist for mates with more symmetrical phenotypes in a variety of different species of animals (Møller 1992a; review in Møller and Swaddle 1997). Furthermore, most parts of the biotic environment including conspecifics, competitors, parasites, predators and food items display properties of symmetry at several different levels (Møller 1992b), and it is easy to imagine that visual perception during the evolutionary past has been tuned to exploit this fact. The existence of a bias in perception of symmetrical characters may also affect perception in other contexts.

Neural system structure

Simple models of neural networks have indicated that a preference for symmetry may arise as a consequence of the way in which the neural system is arranged (Enquist and Arak 1994; Johnstone 1994). The structure of neural systems might allow easier perception of symmetrical than asymmetrical structures. The extent to which this is the case in the current example of insect preferences for floral symmetry depends on whether simple neural network models have any resemblance with the way in which real neural systems and real systems of perception are working (Dawkins and Guilford 1995). More recent computer analyses have revealed that the apparent inherent preference for symmetry in neural networks is a mere consequence of the structure inherent in the presentation regime that the signals underwent, with a sensory bias for homogeneity being the general outcome (Bullock and Cliff 1997). Hence what at first appeared to

be preferences for symmetry as a consequence of the structure of neural networks turned out to be preferences generated by particular procedures of computer programming! Hence hidden preferences in neural networks are unlikely to account for the results of the present study.

Recognition

Insects may not have recognized the asymmetrical objects as flowers. This explanation seems unlikely given that the degree of asymmetry used in the experiment was within the natural range of asymmetry measured in real flowers (Møller and Eriksson 1994, 1995). Since we found the same insect taxa visiting our models as well as real flowers in the same habitats, we see no *a priori* reason for the asymmetrical flower models not to be perceived as flowers in the same way as the symmetrical models.

Radial or bilateral symmetry is common throughout the plant and animal kingdoms, although subtle deviations from symmetry are widespread. Given that organisms may have a partially genetically based control system of developmental stability (Møller and Thornhill 1997), selection against asymmetrical phenotypes may affect the level of morphological asymmetry. The present study of insect preferences for symmetrical flower models, and other studies of the same problem (Horridge and Zhang 1995; Møller 1995a; Møller and Eriksson 1995; Eriksson 1996; Giurfa et al. 1996), suggest that preferential visits of insects to symmetrical flowers comprise one selection pressure for symmetry. Pollinator preferences for symmetrical flowers and assortative visitation of such flowers may also affect plant fitness. Pollen from symmetrical flowers is better at producing zygotes that succeed (i.e. are not aborted), or give rise to mature seeds (Møller 1996; Eriksson 1996), and symmetrical pollen recipients also are better at producing zygotes independent of the phenotype of the pollen donor due to lower rates of seed abortion (Møller 1996, 1997).

In conclusion, flower-visiting insects preferred radially symmetrical flower models over asymmetrical models and larger models over smaller ones, a preference that was independent of pollinator rewards, floral colour, floral odour and flower size.

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