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Insect Choice and Floral Size Dimorphism: Sexual Selection or Natural Selection?

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In considerations of sexual floral size dimorphism, there is a conflict between sexual selection theory, which predicts that larger floral displays attract more pollinators, and optimality theory—particularly the ideal free distribution—which predict that pollinators' visits should match nutritional rewards. As an alternate explanation of this dimorphism, Müller reported that pollinators tend to visit larger male flowers before visiting smaller female flowers, thereby promoting effective pollination. To investigate optimality predictions, I offered pollinators a choice between smaller, less numerous, but more rewarding flowers; and larger, more numerous, but less rewarding flowers. Foragers initially favored the larger and more numerous flowers, but rapidly shifted preferences to conform with the predictions of the ideal free distribution. To test Müller's hypothesis, I offered pollinators choices between larger and smaller corollas of equal caloric reward. Results showed that although pollinators tended to visit larger corollas first, they did not visit them more often. These experiments highlight the need for further investigation into the tradeoff between natural and sexual selection, and their respective influences in pollination ecology.

KEY WORDS: sexual selection; optimality; pollination; floral dimorphism; ideal free distribution.

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INTRODUCTION

Male floral displays are frequently larger than female displays in many plants with imperfect flowers, which had been known well before Darwin's discussion of floral polymorphism (Darwin, 1888). This observation is still noted by modern authors (Baker, 1948; Lloyd and Webb, 1977; Faegri and van der Pijl, 1979; Bell, 1985).

Considering that this floral dimorphism resembles sexual size dimorphism in many animals, Janzen (1977) suggested parallel sexual mechanisms between animals and plants, where larger male flowers would be comparable to larger male animals. Thereafter, Willson (1979) proposed that sexual selection (Darwin, 1871; Maynard Smith, 1991) may be a force in plants as it is in animals. She suggested that larger male corollas and inflorescence sizes—or, for the purposes of this paper, an increased floral display area (FDA)—would attract more pollinators and in turn, sire more offspring. The literature does not specifically designate which of the many sexual selection mechanisms might be involved in this system, but presumably the larger "male" (i.e., pollen donor, even if gynodioecious) FDA is a result of male–male competition (Huxley, 1938), sensory exploitation (Ryan and Rand, 1990), or conceivably a variation of runaway (Fisher, 1915, 1958) in that "preference" might drive the system.

Since then, Willson (1990, 1991, 1994) and other authors (Faegri and van der Pijl, 1979; Queller, 1983; Sutherland and Delph, 1984; Nakamura *et al.*, 1989) have published in support of the concept. Other authors have expanded the theory beyond size dimorphisms (Bawa, 1980a,b; Beach, 1981; Stephenson and Bertin, 1983) and an entire journal supplement explored the various aspects of sexual selection in plants, and their parallels with animals (Arnold, 1994).

However, the original concept—that sexual selection might account for floral size dimorphisms—has not been definitively resolved. A number of researchers have failed to find consistent evidence for sexual selection in FDA dimorphism (Chaplin and Walker, 1982; Kay *et al.*, 1984; Bell, 1985; Firmage and Cole, 1988; Campbell, 1989; Andersson, 1991; Campbell *et al.*, 1991; Eckhart, 1991; Stanton *et al.*, 1991, 1992; Poldolsky, 1993; Conner and Rush, 1996; Broyles and Wyatt, 1995; Emms *et al.*, 1997). Willson had also produced prior work that did not support the concept (Willson and Rathcke, 1974). For these and other reasons, a number of authors have questioned various aspects of sexual selection theory in flowers and plants (Stephenson and Bertin, 1983; Devlin and Stephenson, 1985; Lyons *et al.*, 1989; Wilson *et al.*, 1994; Grant, 1995; Broyles and Wyatt, 1995, 1997).

Researchers applying sexual selection theory to floral dimorphism have generally considered the problem from the perspective of the plant's fitness. But unlike sexual selection in animals, in plants there is no female receiving desired genes by selecting a handsomer male, or by submitting to a superior competitor. In flowers there is a pollinator, who is generally foraging for food.

Considered from the perspective of the pollinator's fitness, natural selection via optimal foraging theory (OFT) offers predictions divergent from those of sexual selection, i.e., pollinators should make foraging decisions based entirely upon nutritional gain per unit time (Pyke *et al.*, 1977; Pyke, 1978; Krebs and Davies, 1993), independent of appearance. Several authors have considered caloric rewards of floral sexes (*vide infra*), but apparently no one has explored the possibility that the predictions of sexual selection are in conflict with those of OFT.

A considerable body of literature exists supporting OFT in pollinators. Pollinators have proven very sensitive to changing caloric rewards (Wainselboim *et al.*, 2002), and authors have shown that in various situations, pollinators either place caloric rewards above appearance or that, given equal caloric payoffs, appearances do not influence pollinator preference (Butler, 1945; Grant, 1966; Free, 1968; Thomson and Plowright, 1980; Heinrich, 1975; Campbell *et al.*, 1991; Mitchell, 1993). In addition, pollinators rapidly switch preferences—not just to different flowers, but to entirely different species—in response to different rewards, irrespective of floral appearances (McGregor *et al.*, 1959; Free, 1968; Pyke *et al.*, 1977; Heinrich, 1976, 1983; Frankie and Haber, 1983; Comba *et al.*, 1999).

Additionally, Darwin never suggested that sexual selection might be an explanation for floral dimorphism in his extensive review of sexual and other polymorphisms in flowers (Darwin, 1888). To the contrary, despite having founded sexual selection theory, Darwin's comments support OFT: "The plants which produced flowers with the largest glands or nectaries, excreting the most nectar, would oftenest be visited by insects, and would oftenest be crossed . . ." (Darwin, 1859, p. 102).

There are at least two alternative hypotheses to sexual selection in floral size dimorphisms. The first would be that male–male competition does not involve FDA, *per se*, but floral rewards. In such a case, FDA would only serve as an advertisement of those rewards, a correlated character. There are a number of researchers who have documented higher nectar production rates from larger flowers (Faegri and van der Pijl, 1979; Harder *et al.*, 1985; Primack, 1987), and there is evidence that nectar reward often increases with flower size both within and among species (Harder and Cruzan, 1990). It is also true that in at least some species, female flowers offer decreased rewards, or even none, compared to males (Kaplan and Mulcahy, 1971; Bawa, 1980a,b; Bell *et al.*, 1984; Ågren *et al.*, 1986; Ashman and Stanton, 1991). The extent to which this nutritional disparity is a factor in intraspecific, intersexual size dimorphism is outside the scope of this paper, but merits further investigation.

Müller (1873) offered another possibility, a "sequence hypothesis," reporting that pollinators preferentially visit larger corollas before visiting smaller ones. He suggested that floral sexual size differences serve to promote effective pollination: If pollinators visit larger, pollen-donating flowers first, and smaller, pollen-accepting flowers thereafter, pollination is enhanced.

This visitation preference could be explained by several mechanisms. First, a larger FDA subtends a larger visual arc. As a pollinator approaches a patch from a distance, it should therefore recognize the larger FDA first visited it before any smaller FDA (Spaethe *et al.*, 2001). Second, it may be that larger FDA generally produces more nectar, as noted previously, attracting pollinators first within a patch.

In addition, authors have noted that pollinators' interest in larger FDA rapidly decays in the morning (Young and Stanton, 1990; Delph and Lively, 1992), and I have unpublished experiments that support this. Such a decay suggests an intriguing third hypothesis, that pollinators are choosing flowers in sequence only until they have acquired sufficient residual pollen load to insure continued fertilization. If so, this points to a more complicated situation, in that pollinators may be selected to maximize food crops for future generations.

Darwin objected to Müller's sequence hypothesis, countering that the smaller size of the female corolla was a result of genetic/physiological mechanisms, specifically, "a tendency to abortion spreading from the stamens to the petals" (Darwin, 1888). Lloyd and Webb (1977) reviewed Müller's hypothesis, and deferred to Darwin's explanation. Darwin's explanation leaves other problems, however, as it negates both sexual selection and the sequence hypothesis.

Darwin's "abortion mechanism" lacks empirical support, and there is at least some evidence against it, as female FDA in some plants is larger than male (see comments on *Solanum* spp. in Discussion). Considered in the light of modern discoveries unavailable to Darwin, his explanation seems highly unlikely. If there is any linkage disequilibrium between the genes controlling stamen and petal development, the two organs should respond to selection independently, eventually arriving at whatever relationship best serves the plant's fitness.

These various ideas invite a reconsideration of the role of sexual dimorphism in floral sizes, and the tension between sexual and natural selection in these systems.

I performed two experiments investigating the problem. The first tests the predictions of sexual selection against those of OFT. The second tests the predictions of sexual selection against those of Müller's sequence hypothesis.

METHODS

In July of 1996, I performed experiments in which native free-flying bumblebees (*Bombus* spp.) were presented with floral options in a patch of 15 althea (*Hibiscus syriacus L.*). The althea were collected from wild seedlings, and are typical of long-established American stocks. The plants were located in Lafayette, Louisiana approximately 50 m from the campus of the University of Louisiana. The shrubs were arranged in a single row approximately 12 m long, running roughly northeast–southwest.

The flowers of althea are lavender and approximately 8 cm in diameter. The corolla is easily trimmed with small surgical scissors to provide different FDAs. An FDA reduction to 40% of normal generates an approximately 5 cm corolla diameter, which is markedly smaller than normal, but still quite large.

The nectaries of althea are readily accessible through gaps between the bases of the five petals. Nectar rewards in all experiments were manipulated using a 0.5 cc syringe with blunted needle to inject a 50:50 sucrose:water solution by volume. Where cut flowers were used, they were presented in florists' picks (i.e., water-bearing tubes with slotted caps for inserting stems) filled with water and Floralife® (Floralife, Inc., Walterboro, South Carolina U.S.A.), mixed to the manufacturer's specifications.

Experiment 1

All flowers were removed from the patch of althea except for two "patchlings" (i.e., subdivisions of one general patch), one on each end of the row.

In the first version, 12 flowers were spared at the northeast end of the row, and circumferentially trimmed to 40% of normal corolla area; at the southwest end, 18 flowers were spared and left full size. In order to manipulate nectar rewards, all flowers were supplemented throughout the experiment with 0.01 ml of artificial nectar as described above. The 12 smaller flowers, however, were supplemented at the beginning of each 15 min observation period, while the 18 larger flowers were supplemented at the beginning of every other 15 min observation period, so that the larger flowers received nectar supplements at half the rate of the smaller.

In the second version, 8 flowers were spared at the northeast end, again trimmed to 40% of normal area, while 12 full-sized flowers were spared at the southwest end. Supplementation schedules were altered from the previous version, such that the 8 smaller flowers were supplemented at the beginning of each 15 min observation period, while the 12 larger flowers were supplemented at the beginning of every third such period, so that the larger flowers received nectar supplements at one-third the rate of the smaller.

Subject flowers in both patchlings faced the same direction, so that all flowers in a patchling could be viewed simultaneously. I counted total bumblebee visits to flowers by shifting my observation post from one patchling to the other after each 15 min observation period.

Because of the many uncontrolled variables of an outdoor experiment utilizing a wild population—temperature, sunlight, humidity, competing food sources, etc.—bumblebee visits varied widely during the day, and even more so from day to day. In addition, the population of visiting bumblebees, and therefore their particular learning curves, did not readily compare from one day to the next. After several exploratory runs, it became apparent that pooling visits from two or more days would prove impracticable, as it would generate formidable obstacles for statistical blocking and analysis.

Therefore I report the data from the first full run of each experiment without repeating the experiments to "fish" for the best data set. Each version of the experiment was run within a single morning, even with the occasional complication of rain. Observations were begun early in the morning, and continued through 10 paired observations, which took about 6.5 h total.

The total number of visits to each patchling was tabulated, and observations were paired chronologically for comparison. Visits to each patchling were calculated as a percentage of the total visits for each paired observation period.

Experiment 2

In the first run, floral wire and floral tape were used to present bumblebees with juxtaposed pairs of uncut flowers, which allowed the flowers to continue natural nectar production. Each pair of flowers contained one full-sized corolla, and one corolla that had been reduced in total area through circumferential trimming by 20, 40, or 60%.

Pollinators, however, have proven sensitive to flower position and direction of approach, and nearby flowers can influence search patterns (Grant, 1966; Janzen, 1971; Pyke, 1978, 1982; Waddington and Heinrich, 1979; Corbet *et al.*, 1981; Thomson *et al.*, 1982, 1989; Haynes and Mesler, 1984; Bell, 1985). Because the floral wire and tape were difficult to apply and rearrange, it was not possible to frequently reverse flower position in order to neutralize such influences. For this reason, a second run was performed. Cut althea flowers were presented in florist's picks filled with water and suspended in a horizontal wire frame, again in pairs, with the same corolla reductions as in the first version. The frame was hung on a shrub from which all other flowers had been removed. This arrangement removed the influences of nearby flowers, and allowed easy reversal of flower positions every 30 min. Cutting mandated that flowers be periodically supplemented with an artificial nectar. Every 15 min 0.01 cc of a 50:50 sucrose:water solution was injected into one nectar chamber of each flower. Thus the flowers in a pair differed in size but presumably not in nectar content.

In both versions, I recorded each pollinator's total visits within the subject area, and which flower was visited first.

RESULTS

Experiment 1

The ideal free distribution (IFD) states that foragers will distribute themselves among reward choices, both temporally and geographically, in consumption ratios that equal, available reward ratios (Krebs and Davies, 1993). If bumblebees are visiting the two patchlings in accordance with IFD, the distribution ratios of their visits should equal nutrition production ratios (Pleasants, 1981; Delph and Lively, 1992; Dreisig, 1995). In the first version, such a visitation schedule would distribute pollinator visits to the "minor" (i.e., smaller but more rewarding) patchling, as described by the following calculation:

$$\frac{12x}{12x + 18(0.5x)} \times 100 = 57\%$$

where x is the amount of nectar injected at each augmentation, and 0.5 in the denominator represents half the total augmentation for the "major" (larger, less rewarding) patchling.

Similarly, the distribution of visits to the minor patchling in the second version would be described by:

$$\frac{8x}{8x + 12(0.33x)} \times 100 = 67\%$$

Figures 1 and 2 show the percentage of visits to the minor patchlings, with the IFD predictions shown as a dashed line. Points were tested against

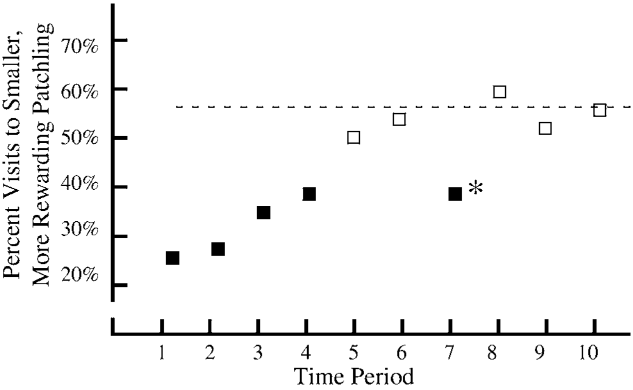

Fig. 1. Experiment 1 (version 1): Percentage of pollinator visits to smaller, less numerous, but calorically more rewarding flowers, as opposed to visits to larger, more numerous, but less rewarding flowers. The *dashed line* represents 57% of visits to the smaller flowers, the response predicted by the ideal free distribution. *Open squares* represent preferences that are indistinguishable from predicted. Bumblebees initially preferred the larger, more numerous flowers, but rapidly switched preference to the more rewarding flowers. The *asterisk* denotes a brief light rain.

predicted by χ^2 goodness of fit. Open squares denote those that were not significantly different from predicted ($p < 0.05$).

Experiment 2

Pollinators' absolute preference for the larger corolla was calculated as:

$$\text{absolute preference} = \frac{\text{total visits to larger flower}}{\text{total visits to both flowers}};$$

and sequence preference was calculated as:

$$\text{sequence preference} = \frac{\text{first visits to larger flower}}{\text{first visits to both flowers}}.$$

Both are presented as percentages in Fig. 3.

In both runs of the experiment, sequence preference was consistently and significantly larger than absolute preference ($p < 0.05$) at both 40 and 60% reductions of the smaller corolla, and non-significant at 20% reduction. Therefore the data from the two runs were pooled and χ^2 was calculated against a neutral (50%) outcome.

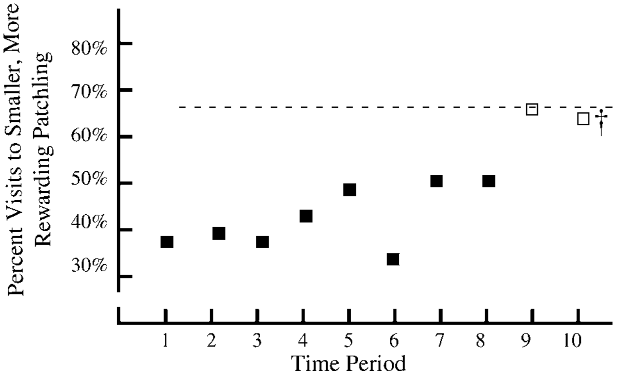

Fig. 2. Experiment 1 (version 2): Same as Fig. 1, but the *dashed line* represents the preference predicted by the ideal free distribution of 67% of visits distributed on the smaller flowers. The *dagger* represents rain that terminated the experiment; data point is extrapolated from rate established before experiment was interrupted.

DISCUSSION

In both experiments, results support concepts of natural selection in predicting pollinator preferences.

In the first experiment, bumblebees initially preferred larger corollas, as evidenced by a low visitation rate to the smaller flowers. With the experience of differing caloric rewards, however, pollinators quickly adjusted their visits and ultimately visited the minor patchling preferentially. The final distribution of their visits to the two patchlings coincided indistinguishably with the predictions of IFD, with no residual preference for larger, more numerous corollas. Sexual selection would have predicted a persistent preference for larger FDA. To date, no one has offered an equation to estimate the strength of sexual selection in FDA dimorphism. Based on the ratios of total FDA, the two experiments would have both predicted visits of 21% to the minor patchling, which is close to the starting data for the first experiment, but not the second. Based on the ratios of flower numbers, both experiments would have predicted visits of 40% to the minor patchling, and this is close to the starting data for the second experiment, but not the first.

These results support the concept that pollinators forage optimally. If pollen donors are sexually competing for optimality-driven pollinators, then that competition should take the form of increased caloric rewards; any increased FDA should only serve as an advertisement of those rewards. So differing rewards might result from sexual selection, but differing

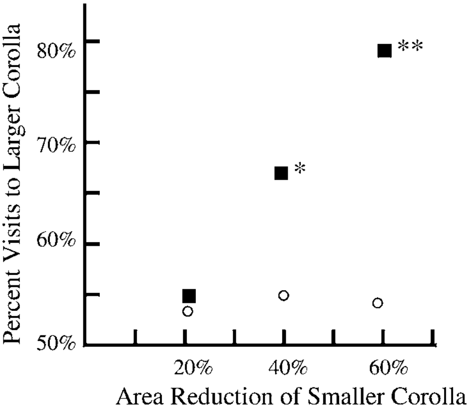

Fig. 3. Experiment 2: Comparison of absolute preference (i.e., percent total visits; open circles) and sequence preference (i.e., percent first visits; solid squares) in pollinator choices between normal corollas and reduced corollas (two runs pooled, see text). All points are tested for difference from "no preference" (50%): a *single asterisk* denotes significant difference ($p < 0.05$); a *double asterisk* denotes highly significant difference ($p < 0.005$).

floral appearances *per se* should not be sufficient to constitute sexual selection/competition. An exception to this might comprise flowers in which there are few repeat visits to flowers. Examples of low-repeater strategies might include scattered, relatively rare flowers that do not generate enough experience for pollinator learning, particularly in pollinators that do not specialize; and systems in which pollinators are seeking benefits other than nutrition, such as deceit-pollinated flowers (Dafni, 1984). This latter system might also be an example of sensory exploitation.

It should be noted that bumblebees may have more learning ability than other pollinators, and would therefore be a poor test case. This is possible but given the ubiquity of competition for limited resources, if two species are competing for a food source, and one is foraging optimally and the second is not, then with time we would expect the optimized forager to drive the other to extinction.

In the second experiment, sexual selection theory presumably predicts a directly proportional relationship between absolute preference and corolla size. It was sequence preference, however, that proved directly proportional to corolla size, while absolute preference remained statistically indistinguishable from neutral (50%). These data therefore support the sequence hypothesis.

In an interesting test case of Müller's hypothesis, in some monoecious species of *Solanum* (a genus in which pollen is the sole reward), male flowers are smaller and hermaphroditic flowers are larger, a reverse of the usual situation (Anderson and Symon, 1989). Sexual selection does not offer an apparent ultimate explanation for this reversal, but the sequence hypothesis might. From the latter theory we can speculate that inbreeding is perhaps a larger problem for this species than most, because in addition to sexual size reversal, the larger, usually single, hermaphroditic flower is generally located distal to the male flowers on a branch. The two conditions together could increase the probability that pollinators will visit the hermaphroditic flower before the male flowers, fertilizing it with pollen from other plants, and promote out-crossing. This would be comparable to mechanisms seen in other plants, such as *Alocasia odora* (Miyake and Yafuso, 2003).

The tension between natural selection and sexual selection is complex, and even Darwin (1871) did not resolve it to his complete satisfaction. Elsewhere (Abraham, 1996) I have suggested a mechanism under natural selection for sexual dimorphism in animals. This paper extends those considerations into plants, with the aim of stimulating further discussion and research into the interplay between the two theories.

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