

EVOLUTION OF A FLOWER DIMORPHISM: HOW EFFECTIVE IS POLLEN DISPERSAL BY “MALE” FLOWERS?¹

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Abstract. Many plants produce more flowers than will set fruit. In some species, a subset of flowers are actually female-sterile and morphologically distinct; these flowers are presumed to enhance fitness primarily through pollen donation. Individual plants of the hummingbird-pollinated shrub *Besleria triflora* produce both long-styled and short-styled flower morphs, characteristic of these “andromonoecious” sexual systems. Short-styled flowers set fruit rarely when hand-pollinated and are therefore functionally staminate. To test the hypothesis that selection for increased male function maintains flower dimorphism, I measured relative pollen dispersal per unit investment by staminate vs. perfect (long-styled) flowers. In the field, anthers of perfect flowers dispersed pollen for a significantly longer time than did those of staminate flowers. In laboratory experiments, hummingbirds transferred more pollen per visit from perfect flowers than from staminate flowers, in part due to differences in flower-morph pollen production. As a result, perfect flowers dispersed substantially more pollen than staminate flowers over an average flower lifetime. The two flower morphs did not differ in the amount of biomass invested through the time of corolla abscission, suggesting that staminate flowers do not conserve resources substantially. These results fail to support the “male-function” hypothesis for the evolution of andromonoecy. Staminate flowers contribute relatively little to plant reproductive success directly through male function, suggesting they are maintained for reproductive functions other than pollen donation.

Key words: *andromonoecy*; *Besleria triflora*; *flower morphology*; *functional gender*; *male function*; *perfect flower*; *pollen dispersal*; *reproductive success*.

INTRODUCTION

Numerous studies have shown that slight variation in floral traits can affect the way a flower contributes to plant reproduction through seed set, pollen donation, and pollinator attraction (Bawa and Webb 1983, Bell 1985, Galen and Stanton 1989, Murcia 1990). In the more specialized “monoecious” sexual systems, individual plants bear distinct flower morphs (Bawa 1979, Lloyd 1979). Presumably, natural selection should maintain distinct flower morphs on individual plants only when each morph performs some reproductive function more effectively than other morphs. However, few studies have experimentally demonstrated such an advantage to floral specialization (Richards 1986).

In the sexual system known as andromonoecy, individual plants produce staminate flowers, which are incapable of seed production, and perfect (hermaphrodite) flowers. Major hypotheses for the evolution and maintenance of andromonoecy emphasize resource allocation (Bertin 1982). When resources limit fruit production, selection should favor individuals that produce a portion of flowers that do not set fruit but that

serve other reproductive functions, such as pollen donation or pollinator attraction. Studies commonly assume that pollen donation is the primary function of staminate flowers (Coleman and Coleman 1982, Pellym 1986, Solomon 1986, May and Spears 1988), which is consistent with the more general hypothesis that plants produce more flowers than can set fruit in order to increase fitness achieved through male function (Sutherland and Delph 1984). However, whereas low fruit-to-flower ratios are common among angiosperm species (Sutherland and Delph 1984), the production of distinct flower morphs is relatively rare (Yampolsky and Yampolsky 1922). This suggests that additional factors are needed to account for the evolution and maintenance of staminate flowers in andromonoecious species.

I examined the reproductive consequences of flower dimorphism in *Besleria triflora* (Gesneriaceae), a self-compatible, hummingbird-pollinated shrub in Costa Rican cloud forest. The production of staminate flowers in *B. triflora* could enhance male reproductive success in two ways: directly, by dispersing pollen more successfully than perfect flowers, or indirectly, by attracting pollinators and increasing pollen dispersal from other flowers better than would a monomorphic display. Using field experiments (Podolsky 1992) I rejected the hypothesis that staminate flowers indirectly enhance pollen dispersal more effectively than perfect

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flowers. In this paper I evaluate direct contributions to male reproduction, and use "male function" to refer specifically to the performance of morphs in pollen donation.

The male-function hypothesis for the evolution of andromonoecy predicts at least one of two benefits regarding the relative efficiency of flower morphs at pollen dispersal. (1) Staminate flowers could disperse pollen more effectively than perfect flowers, either by redirecting resources from pistil development to pollen production (Bertin 1982, Whalen and Costich 1986), or by developing a morphology better suited for pollen dispersal when no longer accommodating female function (van der Pijl 1978). (2) Staminate flowers could cost less to produce (Solomon 1986), especially when pistils are a significant portion of the floral mass (Bell 1985, Cruden and Lyon 1985). Together these potential benefits predict that staminate flowers should disperse more pollen per unit investment than perfect flowers.

Here I describe characteristics of flower morphs, confirm the andromonoecious sexual system of *B. triflora*, and examine relative pollen dispersal by the two morphs. Because it is impractical to gain a field estimate of pollen donation by long-lived flowers (Bertin 1988) I divide the problem into two parts, one that can be addressed in the field ("how long do flower morphs disperse pollen?") and one in the laboratory ("how much pollen do they disperse per visit?"). Combining these measures, I estimate relative pollen dispersal by the two flower types over a typical flower lifetime.

STUDY SITE AND ORGANISMS

This study was conducted at the Monteverde Cloud Forest Reserve (≈ 1600 m) in central Costa Rica ($10^{\circ}18' N$, $84^{\circ}49' W$). *Besleria triflora* (Oerst.) Hanst. is a common understory shrub (1–3 m tall) in virgin lower montane rainforest (Lawton and Dryer 1980). Plants flower from February through July and peak during early wet-season rains or April–May (Feinsinger et al. 1991). No temporal or spatial separation between flower morphs is apparent; staminate flowers are produced throughout the season and are intermixed with perfect flowers on branches (Podolsky 1989). All regularly censused plants within this study population have produced both staminate and perfect flowers, with a positive correlation between numbers of the two morphs on individual plants over a season ($N = 31$, $r_s = 0.71$, $P < .001$).

Flowers have a bright orange, tubular corolla ≈ 15 mm long with an opening diameter of ≈ 3 mm. Perfect flowers are protandrous, opening with four fused anthers at the top of the corolla, concealing a single closed stigma. Pollen is on the undersurface of anthers and is deposited on the top of an inserted hummingbird bill. The stigma is exposed to pollen receipt only after anthers drop to the corolla bottom. The same temporal

change occurs in staminate flowers, but the stigma is positioned deep within the corolla near the ovary. Individual flowers persist in each phase (anthers up vs. down) for one to several days. Throughout this paper, I refer to "male-phase" flowers (staminate or perfect) as those with anthers up, in position to deposit pollen.

Exclusive pollination of *B. triflora* by the short-billed hummingbird *Lampornis calolaema* (Feinsinger et al. 1986) enabled me to evaluate the importance of floral traits in the context of a predictable and highly efficient pollen vector. This avoids complication in interpretation introduced by an unspecialized pollinator fauna (Primack and Lloyd 1980, Coleman and Coleman 1982) or by large variance in pollen transfer due to imprecise flower handling (Levin and Berube 1972, Harder and Thomson 1989). *Lampornis calolaema* is also easily trained in captivity, facilitating experiments to measure pollen transfer between flowers.

METHODS

Flower characteristics.—Over a 1-mo period near the end of peak flowering (May–June) in 1987, I collected 319 flowers from 41 plants from which pollinators had been excluded using nylon bagging. To characterize the distribution of style lengths, I measured the length of the style from the top of the ovary to the stigma tip. To compare anther position in perfect and staminate flowers, I measured the length of the anther from the top of the ovary to the distal tip of the anther. I used male-phase flowers collected haphazardly from the field for use in unrelated laboratory experiments (Podolsky 1992).

To assess dry mass accumulation over the development of floral organs, I dried to constant mass at $60^{\circ}C$ flowers and several characteristic stages of buds and fruits collected from each of 12 plants, and weighed these individually. Dry mass has been used to compare the "cost" of investment in flowers within species (Primack and Lloyd 1980, Bell 1985) and across mating systems (Cruden and Lyon 1985). I also measured the transverse diameter of the ovary for small samples ($N = 18$) of each flower morph.

Female function.—Pollination experiments tested the hypothesis that short-styled flowers would not produce fruit. Throughout the 1988 flowering season I chose from individual plants pairs of staminate flowers that had ended male phase; I supplemented the stigma of one with outcross pollen, leaving the other undisturbed. The outcross pollen came from a single donor plant at least 5 m distant. Flowers were tagged and followed through fruit maturation or abortion.

Male function.—The success of a flower at dispersing pollen depends on the total amount produced, the duration of presentation, the amount removed per visit, and the rate of visitation (Galen and Stanton 1989). To measure the amount and viability of pollen in anthers of both flower morphs, I removed whole anthers from flowers, macerated them in a test tube with 0.5

mL of a neutral-density solution of 3:1 lactic acid: glycerin (P. Diggle, *personal communication*), and counted the number of pollen grains in suspension using a hemacytometer. In addition, I noted the number of pollen grains that were malformed and likely inviable (A. Stephenson, *personal communication*). I averaged counts for two subsamples for each of 12 flowers of each morph.

Anther movements associated with protandry in *B. triflora* clearly define the period of pollen presentation. To measure the duration of male phase I excluded visitors from flowering branches, marked 98 staminate and 88 perfect flowers when they opened and checked every morning until each could no longer deposit pollen on pollinators (i.e., when anthers had dropped at least halfway to the corolla bottom).

From March through May 1988, in the laboratory I measured pollen dispersal from male-phase flowers of the two morphs, using temporarily captive hummingbirds trained to visit hand-held flowers (for training and care methods see Feinsinger and Busby [1987]). Before each set of experiments, the bird was deprived of food for 30–45 min to increase motivation to visit flowers. At the start of a trial I cleaned and dried the bird's bill with a cotton swab. The bird then visited an experimental virgin male-phase flower and then a virgin female-phase perfect flower. After the bird was captured and its bill recleaned, it revisited the male-phase flower and then a new virgin female-phase flower. A complete trial repeated this sequence 11 times. (Due to a limited supply of flowers; I used virgin flowers as pollen recipients only on odd-numbered runs). Thus, pollen deposited on stigmas of six female-phase flowers (runs 1, 3, 5, 7, 9, 11) provided a measure of pollen donation by the male-phase flower over successive visits. Nectar content of the male-phase flower was controlled across visits at 2 μ L of 20% sucrose solution (an average field content; Podolsky 1989). Flowers were collected < 1 d before the experiment from bagged plants in the field.

After each run, stigmas of recipient flowers were severed from styles with a razor blade, softened in a drop of saturated NaOH (9 mol/L) for 24 h, and viewed under epifluorescence to count the number of pollen grains. I measured pollen output by this method for four male-phase flowers of each morph using each of six birds, for a total of 24 trials per flower morph. Results were analyzed with a two-way repeated-measures ANOVA, with number of pollen grains as the dependent variable, flower morph and bird as factors, and visit number as the repeated measure.

Values reported are means \pm 1 standard error.

RESULTS

Flowers showed a bimodal distribution of style lengths, with few of intermediate length (Fig. 1). Many short-styled flowers had reduced or incompletely formed stigmas. In total, 50.8% of 319 flowers in this sample were long-styled (>5 mm) perfect flowers.

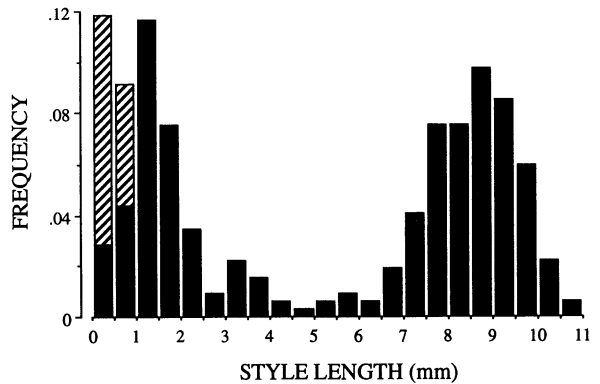


FIG. 1. Distribution of style/stigma lengths among late-season flowers in a population of *Besleria triflora* ($N = 319$). Hatched bars represent styles lacking differentiated stigmatic tissue.

Flower morphs did not differ significantly in ovary diameter (perfect vs. staminate: 2.74 ± 0.07 vs. 2.74 ± 0.10 mm; $N = 18$ each; $t = 0.04$; $P = .96$) or ovary/calyx dry mass (11.61 ± 0.48 vs. 12.28 ± 0.66 mg; $N = 36, 18$; $t = 0.81$; $P = .42$). Most biomass was allocated after fruits began to mature, following the time when staminate flowers would normally abscise (Fig. 2).

In the field, only 2 of 88 (2.1%) naturally visited staminate flowers set fruit (as compared with 37% fruit set for perfect flowers; Podolsky 1989). However, fruit set by staminate flowers was not a function of pollen receipt; fruits were produced by only 1 of 84 pollen-supplemented staminate flowers. These rare instances of fruit set might have resulted from intermediate-length

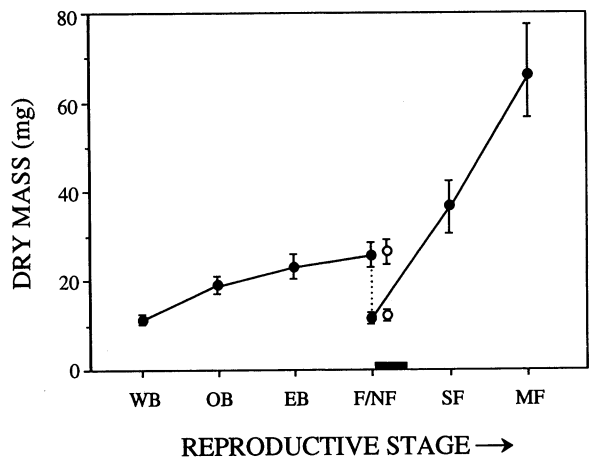


FIG. 2. Biomass accumulation in hermaphrodite reproductive organs at recognizable stages of development. Each point represents the mean value for 12 plants, with each plant represented by the mean value for three organs. The dashed line shows the loss of mass due to corolla drop. For comparison, dry mass of staminate flowers with and without the corolla is shown. Bars represent ± 2 SE. The approximate timing of fruit abortion and staminate flower abscission is shown by the solid bar.

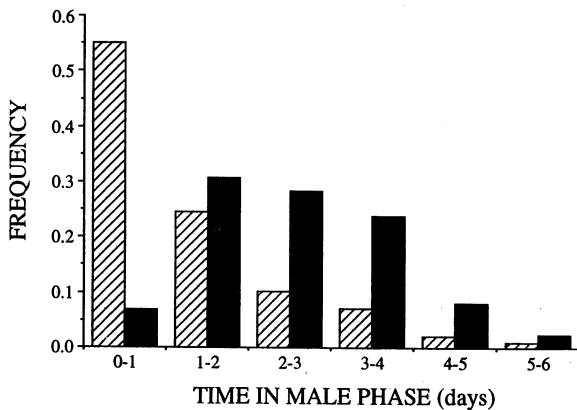


FIG. 3. Duration of male phase for hermaphrodite (■) and staminate (▨) flowers. Mann-Whitney $U = 1816.5$, $P < .001$.

styles that we identified in the field nondestructively as "short" styles (see Coleman and Coleman 1982).

Anthers of staminate flowers stayed in position to disperse pollen for a shorter time than did those of perfect flowers (Fig. 3; Mann-Whitney $U = 1816.5$, $P < .001$). The anthers of most staminate flowers descended within the 1st d. Given that birds do not appear to discriminate between morphs (Podolsky 1989), staminate flowers would therefore receive fewer total visits in male phase than would perfect flowers.

In experiments, hummingbirds transferred significantly more pollen from perfect flowers than from staminate flowers over equal numbers of visits (Fig. 4). Pollen dispersal from both flower morphs declined exponentially over successive visits. Anther length, which could affect pollen delivery by determining pollen placement on the hummingbird, did not differ between morphs (perfect vs. staminate: 9.23 ± 0.25 vs. 8.97 ± 0.23 mm; $N = 40$; $t = 0.77$; $P = .44$). However, anthers of perfect flowers carried almost twice as much pollen ($[4.7 \pm 0.48] \times 10^5$ grains) as those of staminate flowers ($[2.5 \pm 0.23] \times 10^5$ grains; $t = 4.07$, $P < .001$); this difference helps account for the greater than twofold difference in pollen delivery per visit (Fig. 4). The two morphs did not differ in the proportion of pollen grains that were malformed (perfect: $3.2 \pm 0.6\%$; staminate: $3.8 \pm 0.5\%$; $t = 0.85$, $P = .41$).

Given these results, I used the following figures to calculate a rough estimate of relative flower-lifetime pollen dispersal by average flowers of the two morphs. First, median lengths of time in male phase were 2.5 d (perfect) and 0.5 d (staminate; mean = 1.25 d) and flowers receive on average ≈ 4 visits/d (estimated from field observations; Podolsky 1992). This gives an average of 10 visits to perfect flowers and 2 visits to staminate flowers while in male phase. Second, the amount of pollen dispersed per visit declined exponentially according to the regressions reported in Fig. 4. When pollen receipt is summed over the number of visits in male phase, the average perfect flower dis-

perses 4.5–7 times more pollen than the average staminate flower, depending on whether median or mean durations of male phase are used. (This estimate includes pollen delivery to the first female-phase flower; the relative result does not change if pollen carry-over is similar for pollen from the two morphs). Thus, direct contributions to male reproduction by staminate flowers are relatively small.

DISCUSSION

As in other andromonoecious species (Chojnacki 1985), staminate flowers in *B. triflora* open at an immature stage of pistil development. Although some staminate flowers are capable of fruit set, low pollen receipt by the displaced stigma (Podolsky 1989) makes fruit set unlikely. Because they retain complete male structures, however, staminate flowers have been viewed as pollen donors, implying that andromonoecy is driven by selection for increased pollen output (Coleman and Coleman 1982, Pellmyr 1986, Solomon 1986, May and Spears 1988). Past studies have not established, however, that flowers apparently "specializing" on male function are more effective at pollen donation. To the contrary, staminate flowers in *B. triflora* were less effective than perfect flowers both in the length of time pollen was presented and in the quantity of pollen dispersed per visit.

In many andromonoecious species, flower morphs donate equal amounts of pollen, but staminate flowers are more efficiently produced. For example, staminate flowers in *Leptospermum scoparium* were half the dry

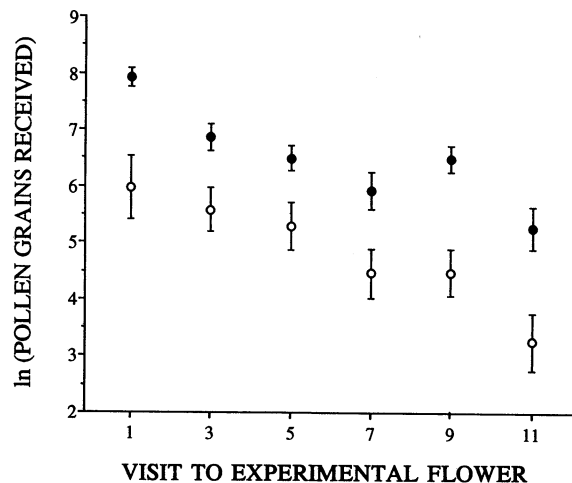


FIG. 4. Number of pollen grains received by female-phase flowers over successive visits to hermaphrodite and staminate male-phase flowers. Values were \ln transformed before analysis. Points are the mean for 24 trials; bars are ± 1 SE across trials. Treatments differed by a two-factor repeated-measures ANOVA ($F = 30.19$, $df = 1, 36$, $P < .0001$). Regression equations used for estimates of flower-lifetime pollen output are: $[\ln(\text{grains}) = 8.0 - 0.43 \cdot (\text{visit number})]$ and $[\ln(\text{grains}) = 6.6 - 0.51 \cdot (\text{visit number})]$ for hermaphrodite and staminate flowers, respectively.

mass of perfect flowers, but dispersed pollen over the same time period (Primack and Lloyd 1980). Flower morphs in *Solanum carolinense* showed equal investment in male structures, including the number of pollen grains, but staminate flowers as a whole were less massive (Solomon 1986). In contrast, ovary size and dry mass did not differ between morphs of *B. triflora*. Although all differences in investment may not be detectable in dry mass (Solomon 1986), pistils in staminate *B. triflora* flowers do not abort early enough to conserve resources substantially. Staminate flowers therefore make a smaller direct contribution to male reproduction than perfect flowers for similar levels of investment.

Given that staminate flowers in andromonoecious species most likely derive from perfect flowers (Bertin 1982, Whalen and Costich 1986), why would species develop and maintain a flower morph with decreased pollen output? One hypothesis is that distributing smaller pollen packages over a greater number of flowers could improve the quality of pollen dispersal by increasing the number of independent dispersal events (Harder and Thomson 1989). However, flower morphs in *B. triflora* overlap spatially and temporally on plants, and it is unclear why staminate rather than perfect flowers would be the target of selection for improved dispersal quality. In fact, the converse is more likely, given that perfect flowers must also devote time to pollen receipt and that the sexual phases are obligately separated in time (cf. Lloyd and Webb 1986). Unless there is some constraint on reducing the pollen content of perfect flowers, this hypothesis is not sufficient to account for reduced pollen in staminate flowers.

Second, genetic correlations could constrain the evolution of female-sterile flowers and result in a correlated decline in pollen output. For example, Breese (1959) found that artificial selection for stigma-anther separation resulted in a correlated response in the relative duration of sexual phases in *Nicotiana rustica*. Limited pistil development in staminate flowers of *B. triflora* could have similar effects on pollen production or male-phase length; other aspects of flower morphology, such as corolla length and diameter, are correlated with style length (Podolsky 1989). However, the existence of genetic constraints would not help to support the male-function hypothesis; clearly, selection on male fitness should not maintain flowers that perform poorly in pollen donation without compensating benefits, such as resource savings, that were not found in this study (Bertin 1982).

Finally, staminate flowers could serve functions other than direct pollen donation, such as increasing pollinator visitation at plants via enhanced attraction (Bertin 1982). In this case, reduced contact with pollinators in a portion of "neuter" flowers (e.g., through the early descent of anthers) could improve outcross pollen receipt by fertile flowers (Lloyd 1979, Bell 1985). In field experiments with *B. triflora* (Podolsky 1992) I

found support for the hypothesis that staminate flower morphology is better suited for an attractive role than is the morphology of perfect flowers. Increased attractiveness benefits female rather than male reproduction, however, indicating that staminate flowers do not strongly enhance male fitness either directly (this paper) or indirectly (Podolsky 1992). Together, these results indicate that enhanced male function is not necessary for the evolution of andromonoecy.

Much recent work has stressed the importance of measuring functional gender of plants, as opposed to inferring gender from phenotypic traits (Horowitz 1978, Lloyd 1980, Robbins and Travis 1986). Traditionally, floral sex expression has also been classified by the possession of mature reproductive parts (Wyatt 1983). This study demonstrates the importance of measuring functional gender of flower morphs by their actual, rather than apparent, contributions to plant reproduction (Bawa and Webb 1983). Analyzing functional gender at the level of both the whole plant and the individual flower is necessary to better understand patterns of resource allocation to floral tissue (Charlesworth and Charlesworth 1981, Charnov and Bull 1986) as well as the evolution of plant sexual systems (Bawa and Beach 1981, Wyatt 1983, Podolsky 1992).

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