

Strange Floral Attractors: Pollinator Attraction and the Evolution of Plant Sexual Systems

Robert D. Podolsky

Individual plants of hummingbird-pollinated *Besleria triflora* display two flower morphs: staminate flowers, which have shortened styles and do not produce fruit, and hermaphrodite flowers. Experiments with *B. triflora* indicate that pollinator attraction can drive the evolution of a dimorphic plant sexual system. In field-manipulated plants, visitation increased at large floral displays; however, pollen receipt increased only when staminate flowers were used to enlarge the display. Laboratory experiments showed that staminate flowers do not remove pollen from visiting pollinators, effectively concentrating outcross pollen onto stigmas of fertile flowers. A dimorphic sexual system is favored because the morphology of staminate flowers enhances their role in pollinator attraction.

To understand the great diversity of floral traits among angiosperms, pollination biologists have focused increasingly on the complex dynamics of pollinator behavior (1, 2). The indirect role of flowers in pollinator attraction—as opposed to the direct role in gamete production—has been invoked more explicitly in understanding resource allocation to floral tissue (3) as well as the influence of floral displays on pollinator visitation (4, 5). Increased attractiveness to pollinators has also been cited in the evolution of a diverse group of sexual systems in which morphology and reproductive function vary among flowers displayed on a plant (2). However, the role of pollinator attraction in maintaining a dimorphic sexual system has not been shown experimentally.

Andromonoecy is a floral-dimorphic sexual system in which individual plants display staminate flowers, which do not develop fruit, and hermaphrodite (bisexual) flowers. The evolution and maintenance of staminate flowers is commonly assumed to be driven by selection for enhanced pollen output (6). However, in the hummingbird-pollinated shrub *Besleria triflora*, staminate flowers disperse substantially less pollen than do hermaphrodite flowers (7, 8). Moreover, staminate flowers position the stigma and anthers away from pollinators for much of the flower life (9). Persistence in an apparently “neuter” phase suggested that staminate flowers could be produced chiefly for their role in pollinator attraction rather than in pollen donation (10). I used field and laboratory manipulations to test this hypothesis.

Experiments were conducted at the Monteverde Cloud Forest Reserve in central Costa Rica (11, 12). In field experiments, I controlled the numbers and types of flowers displayed on plants (13) and then

recorded visitation frequency and pollination success for focal flowers on each plant (14). Three treatments compared pollination success of five focal hermaphrodite flowers when displayed alone (treatment A), with five hermaphrodite flowers (B), or with five staminate flowers (C) (15). The treatments were applied sequentially to each of 12 experimental plants in a Latin-square crossover design (16). For each trial, I recorded the number of flowers probed by each visitor during a 4-hour period 5 days after the start of the treatment. I then measured pollen receipt over 29 hours by four virgin female-phase hermaphrodite flowers. I estimated pollen dispersal by labeling with fluorescent dye the anthers of two male-phase hermaphrodite flowers and measuring over 24 hours dispersal to flowers of neighboring plants (17).

Treatments differed significantly in the average number of visits received per flower (Table 1). Flowers on plants displaying ten

flowers (treatments B and C) were visited more often than those on plants displaying five flowers (A). Treatments B and C increased visitation rates by increasing the rate of pollinator arrivals rather than the proportion of flowers visited per arrival (Table 1). Thus, pollinators made more frequent independent visits to plants with larger displays.

Despite differences in visitation, dye dispersal from focal flowers did not differ significantly among treatments (Table 1) (18). However, the number of pollen grains received by stigmas of focal flowers did differ significantly among treatments (Table 1). Pollen receipt was greater (planned comparisons) in the mixed-flower treatment (C) than in either treatment with only hermaphrodite flowers (A and B). Similarly, the number of pollen tubes in styles of focal flowers differed among treatments, both for analysis of variance and for planned contrasts (19).

In laboratory experiments, I tested a potential mechanism for these differences in pollen receipt. Using temporarily captive hummingbirds (20) as pollen vectors, I compared the effects of intervening visitation at staminate as opposed to hermaphrodite flowers on outcross pollen receipt by subsequent flowers (21). Aspects of morphology (22) suggested that staminate flowers would physically interfere less with pollen movement between flowers than would hermaphrodites. The experiments measured the amount of pollen transferred from a male-phase (outcross) “donor” flower to three female-phase “recipient” flowers, when visits to two “experimental” flowers intervened between donor and recipients (23).

Table 1. Adjusted means (16) for variables measured for three treatments in field experiment. Visitation data were collected over 4 hours, male data over 24 hours, and female data over 29 hours. Raw measurements were transformed where necessary before analysis to improve normality of residuals; means were detransformed after analyses. *F* values and *P* values are for the treatment term in the analysis of variance; no interactions between treatment and other factors were significant. Means in a row marked by different lowercase letters are significantly different at *P* = 0.05 according to the planned comparisons (15).

| Variable | Adjusted means* | | | SE† | $F_{(2,6)}$ | P |
|-----------------------------|--------------------|---------------------|---------------------|-----------|-------------|-------|
| | A (5H) | B (10H) | C (5H, 5S) | | | |
| <i>Visitation</i> | | | | | | |
| Visits per flower | 1.30 ^a | 2.25 ^b | 2.04 ^b | 0.1 | 25.5 | <0.01 |
| Bird arrivals | 2.34 ^a | 4.13 ^b | 3.36 ^b | 0.3 | 8.79 | <0.03 |
| Percent visited per arrival | 63 | 56 | 65 | 8 | 0.16 | >0.75 |
| <i>Male function</i> | | | | | | |
| Median number dye particles | 21.5 | 25.0 | 14.0 | 0.52 (ln) | 0.34 | >0.50 |
| Total number dye particles | 497.7 | 1199.9 | 992.3 | 0.58 (ln) | 0.63 | >0.50 |
| <i>Female function</i> | | | | | | |
| Mean number pollen grains | 756.3 ^a | 1075.8 ^a | 2162.3 ^b | 3.38 (sq) | 8.45 | <0.05 |
| Mean number pollen tubes | 529.0 ^a | 818.0 ^a | 1689.2 ^b | 3.83 (sq) | 5.79 | <0.04 |

*Treatments are the number of hermaphrodite (H) and staminate (S) flowers maintained on the experimental plant. †Standard errors are for means before detransformation, and the type of transformation is indicated as natural log (ln) or square root (sq).

Department of Zoology, University of Florida, Gainesville, FL 32611. Present address: Department of Zoology (NJ-15), University of Washington, Seattle, WA 98195.

As predicted, pollen delivery to the three recipient flowers was greater when the intervening flowers were staminate (Fig. 1). To determine whether staminate flowers interfered at all with pollen transfer, I also compared pollen delivery to the first three hermaphrodite flowers (experimental or recipient) visited in each sequence. Intervening visitation at staminate flowers had no measurable effect on pollen delivery to subsequent flowers (Fig. 1).

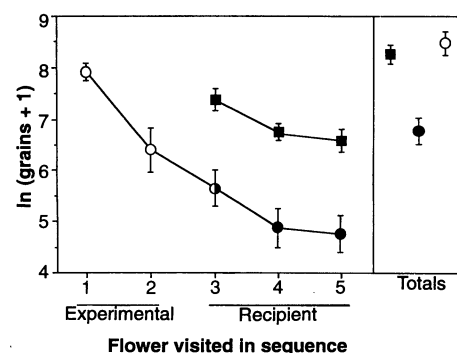
Staminate flowers thus play an indirect but effective role in female reproduction of *B. triflora*. When floral displays were increased experimentally, pollinators visited more frequently and made more probes per flower. However, pollen receipt increased only when staminate flowers had been used to enlarge the floral display. Laboratory experiments demonstrated the passive role of staminate flowers: they do not dilute the greater amount of outcross pollen delivered to fertile flowers. Because flowers on a plant share a limited pollen supply (14), the addition of hermaphrodite flowers would simply increase the number of flowers receiving inadequate pollen loads (24). Thus, plants displaying both flower morphs benefited from more frequent pollen delivery and from the increased concentration of pollen onto the stigmas of a restricted set of fertile flowers (14).

Pollinator attraction has been proposed as an important force in the evolution of specialized sexual systems such as andromonoecy (2, 10). Two results from my experiments validate this hypothesis. First, greater visitation at larger floral displays resulted in a demonstrable reproductive benefit (increased pollen receipt) for pollen-limited *B. triflora* (14, 21, 25). Second, a specialized flower morph was more effective in this role than the more typical hermaphrodite flower. Small changes in development and morphology contribute to this difference in effectiveness (22). Once their anthers have withered, staminate flowers serve as "floral flags" (26) that advertise the plant, but they do not participate directly in reproduction.

The incidence of "morphologically male" flowers serving primarily to attract pollinators is unknown; studies rarely undertake a comprehensive comparison of flower morphs with regard to all aspects of flower function (10). Bertin (10) suggested several plant characteristics that could favor this pattern, including few stamens per flower, protandry, and the use of visually oriented pollinators (traits shared by *B. triflora* and other andromonoecious species). The specificity of the relation between *B. triflora* and its sole pollinator (20) could also be important in maintaining andromonoecy by attraction (27).

One unresolved issue is why, contrary to theory (28), increased visitation benefits

Fig. 1. Number of pollen grains transferred by hummingbirds from a donor flower to a sequence of recipient flowers in laboratory experiments. Intervening between the donor and recipients were visits to two experimental staminate flowers (squares) or hermaphrodite flowers (circles). Pollen receipt is shown for all hermaphrodite flowers (experimental and recipients) averaged over replicates, and bars indicate 1 SE. All values were natural logarithm-transformed before analysis. Pollen on staminate stigmas (flowers 1 and 2 in staminate treatment) was negligible and is not shown. Total pollen grains on three recipient stigmas was significantly greater in the staminate treatment (solid square) than in the hermaphrodite treatment (solid circle; analysis of variance: treatment factor $F[1, 36] = 26.37$, $P < 0.0001$; bird factor, not significant; bird \times treatment interaction, not significant). Total pollen grains on the first three flowers in the hermaphrodite treatment (open circle; analysis of variance: treatment factor $F[1, 36] = 0.78$, $P = 0.385$; bird factor, not significant; bird \times treatment interaction, not significant).



female rather than male pollination success in *B. triflora*. This reversal could result from the large number of ovules per flower (up to 6000) and the high frequency with which flowers receive inadequate pollen for full seed set (11). In this species, more than twice as many visits were needed to fertilize a given fraction of ovules than to remove the same fraction of pollen from anthers (11), indicating that pollen receipt may be the less efficient process. Arguments predicting benefits for male reproduction (28) may be more appropriate for species with few ovules per fruit. When the risk of inadequate pollen receipt is high, investment in attractive structures (in this case, specialized flower morphs) may be advantageous for improving female reproduction (29).

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- Although the two morphs are equal in mass, pollen dispersal is six times as great by hermaphrodite flowers, which produce more pollen and
- present it over a longer period (8).
- R. D. Podolsky, in preparation.
- Besleria triflora* (Oerst.) Hanst. (Gesneriaceae) is a 1- to 3-m-tall shrub. Flowers are bright orange and have a tubular corolla (≈ 1.5 cm in length) typical of hummingbird-pollinated species. Both flower morphs are protandrous, opening with anthers raised to deposit pollen on top of an inserted hummingbird bill. On average, anthers drop out of position to disperse pollen within 1 day (staminate) or 3 days (hermaphrodite) (8). Flowers last 5 to 10 days. In staminate flowers, a shortened style positions the stigma out of reach of pollen receipt. A member of the African violet family, the genus *Besleria* is comprised of ≈ 200 species in the tropical Americas and has not been reported to show this type of flower dimorphism (H. Wiehler, personal communication).
- Aborted pistil development and appearance on plants late in the flowering season (11) are typical of staminate flowers in andromonoecious species and suggest derivation from strictly hermaphrodite flower production [R. I. Bertin, *Evol. Theory* **6**, 25 (1982); M. D. Whalen and D. E. Costich, in *Solanaceae: Biology and Systematics*, W. D'Arcy, Ed. (Columbia Univ. Press, New York, 1986), p. 284; A. J. Richards, *Plant Breeding Systems* (Allen & Unwin, London, 1986)].
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- Experiments were conducted in the latter half of the flowering season during the dry-wet season transition (May to June) in 1988. See (8) and (11) for other details of plant biology and R. Lawton and V. Dryer [*Brenesia* **18**, 101 (1980)] for descriptions of the reserve and its vegetation.
- I "removed" surplus flowers from experimental plants by bagging them in green nylon netting. In several cases, I "added" flowers from flowering branches of other plants, which were suspended in bottles containing half-strength Floralife (Floralife, Burr Ridge, IL) solution. Bottled branches secreted nectar and were not discriminated against by hummingbirds [P. Feinsinger, H. M. Tiebout III, B. C. Young, *Ecology* **72**, 1953 (1991)].
- I measured pollination success per flower because fruit set appears limited by nutrient resources (30 to 40%, regardless of pollination level), whereas seed set per retained fruit (≈ 3000 ovules) is limited by pollen receipt (11). Thus, the pollination success of a subset of focal flowers is a relevant measure of female reproduction.
- The proper number and type of flowers were maintained throughout each 10-day treatment. Treatment C (five hermaphrodite and five staminate flowers) represented the median number of both morphs naturally displayed on plants at the time of the experiment.

16. The 12 experimental plants were arranged into four blocks of three, with three time periods. The design controls for variation caused by plant identity, location within the reserve (block), time of treatment, and carryover of effects (on visitation) from previously applied treatments [R. G. Petersen, *Design and Analysis of Experiments* (Dekker, New York, 1985)]. I used the Tukey test [J. H. Zar, *Biostatistical Analysis* (Prentice Hall, Englewood Cliffs, NJ, 1984)] to test two pairs of a priori pairwise predictions. To examine whether pollinators responded to increases in flower number, I tested the prediction $C = B > A$ for visitation data. To examine effects on pollination success, I tested $C > B = A$ for data on pollen receipt and dispersal.
17. The initial 5 days allowed local pollinators to adjust to the treatment. Residual effects of conditions preceding each treatment were controlled for by the experimental design as well (16). Pollen grains and pollen tubes were measured by epifluorescent microscopy (8). For a given treatment, grains and tubes were averaged over all intact stigmas and styles, respectively. Fluorescent dye has been used successfully to mimic relative pollen movement [S. N. Handel, in *Pollination Biology*, L. Real, Ed. (Academic Press, Orlando, FL, 1983), p. 163; N. M. Waser, *Funct. Ecol.* 2, 41 (1988)]. Twenty-four hours after dye application, I collected stigmas of all female-phase flowers on conspecific plants within 20 m, a sufficient distance to detect most dye movement from other flowers pollinated by *Lampornis calolaema* [Y. B. Linhart, W. H. Busby, J. H. Beach, P. Feinsinger, *Evolution* 41, 679 (1987)].
18. Pollen dispersal was estimated in two ways: the median number of dye particles reaching stigmas of "visited" neighborhood flowers (those receiving at least one dye particle) and the total number of dye particles on these stigmas.
19. I could not assess treatment effects on seed production because many fruits aborted. This was partly an artifact of limiting pollen receipt to 1 day, substantially less than a natural exposure of 3 to 4 days.
20. Recently captured male hummingbirds (*L. calolaema*), the sole pollinator for *B. triflora* (11), were used in experiments. Details on the training and handling of birds are given in (8).
21. A simple model (11) suggests that a larger floral display will improve outcross pollen receipt per flower only if greater visitation compensates for the increased dilution of pollen among flowers. This experiment tested one assumption of the model: staminate flowers would dilute pollen loads delivered to target flowers less than would hermaphrodite flowers.
22. The short male phase, displaced stigma, and shorter and wider corolla of staminate flowers (8) could reduce flower contact with pollinators, limiting pollen removal from the pollinator during visits [C. Murcia, *Ecology* 71, 1098 (1990)]. Greater longevity on plants, despite a shorter male phase, also extends the period during which a staminate flower serves only to attract pollinators (8).
23. In each trial, a bird (with a cleaned bill) visited these six flowers in sequence. Experimental flowers were either both hermaphrodite or both staminate; donor and recipient flowers were hermaphrodite. To avoid confusing the pollen source, I used experimental flowers in which the male phase had ended. Four trials were run for each treatment with each of six birds ($n = 24$ runs per treatment). After each trial, stigmas of all experimental and recipient flowers were treated (8) and viewed under epifluorescence to count pollen grains.
24. Because *B. triflora* exhibits strong inbreeding depression (R. Podolsky, unpublished data), plants could also benefit by avoiding increased within-plant pollination that would result from the addition of hermaphrodite flowers, which have an extended period of pollen dispersal (8).
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26. E. W. Stiles, *Am. Nat.* 120, 500 (1982).
27. D. W. Schemske and C. C. Horvitz, *Science* 225, 519 (1984).
28. Large maternal investment in fruits and seeds suggests that allocation to attractive tissue is chiefly paternal, which has prompted the argument that increased pollinator attraction should benefit pollen dispersal rather than pollen receipt (3, 4).
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Middle Tertiary Volcanism During Ridge-Trench Interactions in Western California

Ronald B. Cole and Asish R. Basu*

Bimodal volcanism in the Santa Maria Province of west-central California occurred when segments of the East Pacific Rise interacted with a subduction zone along the California margin during the Early Miocene (about 17 million years ago). Isotopic compositions of neodymium and strontium as well as trace-element data indicate that these volcanic rocks were derived from a depleted-mantle (mid-ocean ridge basalt) source. After ridge-trench interactions, the depleted-mantle reservoir was juxtaposed beneath the continental margin and was erupted to form basalts. It also assimilated and partially melted local Jurassic-Cretaceous sedimentary and metasedimentary basement rocks to form rhyolites and dacites.

The middle Tertiary geologic history of western California was largely influenced by tectonic events that occurred when segments of the East Pacific Rise interacted with a subduction zone along western North America (Fig. 1). This interaction resulted in the development of the San Andreas fault system (1). Coeval with the ridge-trench interactions were episodes of near-trench volcanism and localized development of sedimentary basins (1-3). Ridge-trench interactions can be important events in the geological evolution of continental margins (4-11). They can also invoke geologic responses such as near-trench volcanism that are in marked contrast to typical subduction processes. Isotopic and geochemical compositions of such near-trench volcanic rocks can provide important information on the magmatic and tectonic processes that take place when a spreading ridge encounters a continental margin. Several studies on volcanic rocks in western California (12-14) have suggested a possible relation between mid-ocean ridge magmas and near-trench volcanic activity. However, these studies either lack a combination of isotopic petrogenetic indicators (for example, combined Nd and Sr isotopic data) or do not contain sufficient data to define a mid-ocean ridge basalt (MORB) end-member composition. In this report we describe Nd and Sr isotopic data that indi-

cate that early Miocene volcanism in the Santa Maria Province (SMP) of west-central California was a direct result of ridge-trench interactions.

The SMP is located along onshore and offshore west-central California. Onshore it is bound by the Nacimiento and Rinconada faults to the east and north, the Santa Ynez fault to the south, and the coastline to the west (Fig. 2) (15). We studied tuff and basalt in the Obispo Formation and tuff in the Lospe Formation, the Tranquillon volcanic rocks, the Catway basalt, and the Lopez Mountain basalt (Fig. 2). The SMP volcanic rocks are bimodal and include basalts and basaltic andesites with rhyolites and dacites. Ages of eruption of the SMP volcanic rocks are mostly between 16 and 18 million years ago (Ma) (16). Available seismic and well-log data for the onshore and offshore SMP reveal that lower Miocene volcanic rocks are volumetrically significant and thicken into normal-fault-bounded basins (17). The short age span and the similar stratigraphic positions occupied by these volcanic rocks (18) suggest that they were erupted rapidly along the continental margin in close association with crustal extension and basin development.

Immediately before Santa Maria volcanism, ~19 Ma, segments of the East Pacific Rise between the Pioneer and Murray fracture zones intersected the continental margin (Fig. 1) near the paleolatitude of the SMP (1, 19). When segments of the East Pacific Rise intersected North America, subduction beneath the continental margin

Department of Geological Sciences, University of Rochester, Rochester, NY 14627.

*To whom correspondence should be addressed.