

Resolution of male–female conflict in an hermaphroditic flower

A. Elizabeth Fetscher†

Department of Biology, University of California, San Diego, La Jolla, CA 92093, USA

The flowers of most angiosperm species are hermaphroditic. Spatial separation of male and female organs within a flower (hercogamy) is a common character traditionally interpreted as an adaptation to reduce intrafloral self-fertilization, one potential cost of hermaphroditism. Another possible cost that may lead to selection for hercogamy is physical interference between male and female floral functions. Here, I present evidence demonstrating the role of a floral character in reducing female interference with male function. The bi-lobed stigma of the bush monkeyflower closes after receiving pollen, causing increased spatial separation of the anthers and stigma ('movement' hercogamy). Experimental manipulations show that flowers with closed stigmas export more than twice as much pollen to other flowers as those in which the stigma is prevented from closing. However, stigma closure only minimally reduces the potential for intrafloral self-pollination. This study provides the first experimental evidence that selection to reduce intrafloral male–female interference can be a strong selective force and can drive the evolution of floral characters usually interpreted as mechanisms to reduce self-fertilization.

Keywords: floral evolution; hercogamy; hermaphroditism; *Mimulus*; self-pollination; stigma–pollen interference

1. INTRODUCTION

Approximately 80% of angiosperm species produce flowers that both receive and export pollen (Proctor *et al.* 1996). Floral hermaphroditism affords the plant an economy of resources because pollinator-attracting features and rewards serve the dual roles of promoting both male and female floral functions (Charnov *et al.* 1976; Givnish 1980). However, the advantages of hermaphroditic flowers may not come without a cost. When male and female parts are housed together within a flower, there is a risk of intrafloral self-fertilization and subsequent inbreeding depression (Charlesworth & Charlesworth 1987). Another, less frequently considered, disadvantage of hermaphroditism is the potential for physical interference between male and female floral functions (Lloyd & Webb 1986; Webb & Lloyd 1986; Bertin & Newman 1993), which stems from the need for flowers to deposit pollen on a part of the pollinator's body that will subsequently contact another flower's stigma. The closer the male and female organs are to one another within a flower, the more likely one is to block the other's access to the pollinator. In addition, female organs may knock freshly collected pollen off a retreating pollinator, or self-pollen deposition may reduce the access of outcross pollen to ovules (Galen *et al.* 1989; Waser & Price 1991; Broyles & Wyatt 1993; Dinnétz 1997; Sage *et al.* 1999). Finally, if interference by the stigma reduces the flower's ability to export pollen to others, then a reduction in hercogamy that increases the selfing rate might also increase interference, causing a loss of male outcrossing success, a phenomenon known as pollen discounting (Holsinger *et al.* 1984).

The separations of stigma receptivity and pollen release within a flower in space (hercogamy) and time

(dichogamy) are very common characters among hermaphroditic plants. Over two centuries ago, Sprengel (1793) published the idea that some floral characters serve as a means of reducing interference between pollen receipt and export, and some recent authors have interpreted hercogamy and dichogamy in this light (Lloyd & Webb 1986; Webb & Lloyd 1986; Bertin & Newman 1993). However, much more attention has been paid to the hypothesis (Darwin 1876) that floral traits such as hercogamy and dichogamy have evolved as mechanisms to reduce the frequency of intrafloral self-fertilization (Schoen 1982; Barrett & Shore 1987; Holtsford & Ellstrand 1992; Brunet & Eckert 1998). Examination of the interference hypothesis has focused largely on the role of self-pollen deposition in reducing the access of outcross pollen to ovules (Galen *et al.* 1989; Waser & Price 1991; Broyles & Wyatt 1993; Campbell *et al.* 1994; Dinnétz 1997; Sage *et al.* 1999). Although one published study prior to this one has explicitly examined the hypothesis that floral characters are adaptations to reduce intrafloral interference with pollen export by female organs (Kohn & Barrett 1992), it did not yield support for the hypothesis. Here, I present the first research to demonstrate that a floral trait functions to reduce intrafloral male–female interference.

The bi-lobed stigma of the bush monkeyflower (*Mimulus aurantiacus* (Scrophulariaceae)) closes rapidly (*ca.* 2 s) in response to touch by a hummingbird pollinator, moving out of the way of the anthers (figure 1). Touch-sensitive stigma closure is common in at least four families in the order Scrophulariales: Scrophulariaceae, Bignoniaceae, Martyniaceae and Lentibulariaceae (Newcombe 1922). Webb & Lloyd (1986) categorized stigma closure as 'movement' hercogamy because closure brings about additional separation between sex parts. They suggested that stigma closure reduces interference between male and female functions, in contrast to the more common interpretation that it promotes outcrossing

†Present address: Department of Biology, University of California Riverside, Riverside, CA 92521, USA (annef@mail.ucr.edu).

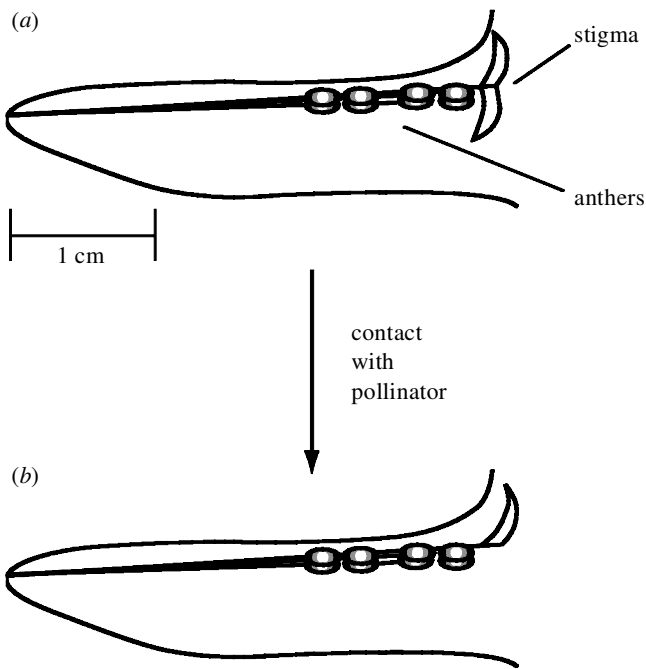


Figure 1. Diagram of a bush monkeyflower with its stigma in (a) the open and (b) the closed positions. Though both stigma lobes respond to touch, hummingbirds usually contact only the lower one, such that it is the one that moves, resulting in the closed stigma being reflexed upward.

by reducing intrafloral pollen transfer during a pollinator's visit (Kerner von Marilaun 1895; Newcombe 1922, 1924; Lloyd & Yates 1982). Ritland & Ritland (1989) examined the latter hypothesis by measuring the correlation between the speed of stigma closure and the outcrossing rate in several *Mimulus* species but they were unable to establish a significant relationship between the two factors.

Pollinated stigmas of the bush monkeyflower usually remain permanently closed, even when less pollen is received than is required for full seed production. However, if fewer than one-third of the ovules are fertilized, some stigmas do reopen and these are able to receive additional pollen, which contributes to increased seed production (Fetscher & Kohn 1999). Why, then, would underpollinated stigmas forgo future opportunities for pollen receipt by remaining closed? Here, I test the hypothesis of a trade-off between male and female functions, such that flowers with closed stigmas realize higher fitness through male function (pollen export) per hummingbird visit than flowers with open stigmas. I use experimental manipulations of stigma closure to study its effects on both pollen export and self-pollen deposition. The results provide strong evidence that selection to reduce interference between pollen receipt and pollen export can be an important force in the evolution and maintenance of floral characters.

2. METHODS

All experiments were carried out at the University of California's Dawson Los-Monos Canyon Reserve in Vista, California, between May and August 1996–1998 using the bush monkeyflower, a self-compatible shrub. A large population of bush

monkeyflowers is present at the Reserve and is visited by several species of hummingbird pollinators: Anna's (*Calypte anna*), black-chinned (*Archilochus alexandri*), Allen's (*Selasphorus sasin*), Costa's (*Calypte costae*) and rufous (*Selasphorus rufus*).

(a) Pollen export

To study the effect of stigma closure on pollen export, free-ranging hummingbirds in a habitat containing bush monkeyflowers were provided with artificial inflorescences at which to forage. Each inflorescence consisted of a branched, upright wooden framework to which were attached six florist's vials, each containing one previously unvisited bush monkeyflower. One flower on the inflorescence served as a pollen donor and the remaining flowers were available to serve as potential pollen recipients. Anthers were removed from these latter flowers to prevent pollen transfer between them. Donor flowers had dehiscent anthers and received one of three stigma treatments: the stigma was either closed by touch prior to hummingbird visitation, open but able to close (unmanipulated), or propped open and made unable to close by affixing a light cloth mesh, cut to size, to its open surface using a thin coat of Elmer's school glue (Elmer's Products, Inc., Columbus, OH, USA) (figure 2a). The mesh was necessary to hold the stigma open, in its natural shape, while the glue was drying. The closed-stigma treatment, which reflects the natural situation in which the flower has already been visited and the stigma has closed, was employed to test the hypothesis that the open stigma impedes the anthers' access to a foraging hummingbird. The propped-open-stigma treatment prevents stigma closure without disturbing the undersides of the stigmatic lobes, which are hypothesized to interfere with pollen export by removing freshly collected pollen from the retreating bird in a single visit. Stigma treatments were assigned to flowers at random, in order to eliminate systematic biases from any aspects of floral biology that could otherwise influence pollen export. In preparation for each hummingbird foraging bout, the inflorescence was stocked with fresh flowers. During each bout, the order in which the flowers were probed was recorded and hummingbird visits to pollen-donor flowers were videotaped at close range. Anthers in the bush monkeyflower spring open to release pollen in response to touch by a pollinator. Following each foraging bout, the donor flower was examined to determine whether the anthers had been contacted and, if so, the stigma of the first recipient flower pollinated following visitation to the donor flower was collected for subsequent determination of pollen load under a microscope. Although any increase in pollen export afforded by stigma closure could result in increased pollen receipt by several of the flowers visited subsequently due to pollen carryover (Webb & Bawa 1983; Thomson *et al.* 1986), I focused on pollen loads received by the first recipient only. This method provides a conservative estimate of the degree to which stigma closure increases pollen export from a donor flower.

(b) Self-pollen deposition

An alternative hypothesis to explain stigma closure is that it reduces intrafloral self-pollination. To assess the potential for intrafloral pollen deposition in the absence of stigma closure, hummingbirds were trapped in a 1.5 m × 3 m × 2 m aviary, cleaned of any pollen with a damp cotton swab and allowed to forage at an artificial inflorescence inside the aviary. The inflorescence bore a previously unvisited experimental flower, with dehiscent anthers, whose stigma was held open with a dab of Elmer's school glue (Elmer's Products, Inc.) on the back of each

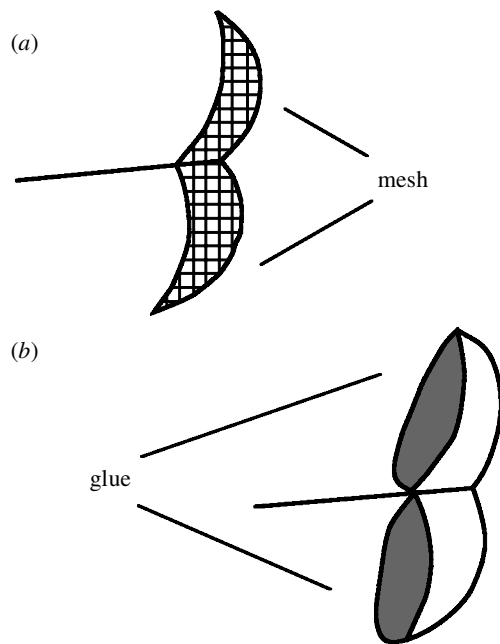


Figure 2. Close-ups of a bush monkeyflower stigma manipulated to prevent closure by (a) application of a light mesh glued to the receptive surfaces, for the pollen-export experiment, and (b) application of Elmer's school glue (Elmer's Products, Inc.) to the undersides of each lobe, for the self-pollen deposition experiment.

stigmatic lobe (figure 2b). This manipulation prevents closure but retains the natural morphology of the receptive surface of the open stigma and does not affect pollen receipt in the field (Fetscher & Kohn 1999). Following a hummingbird's visit to the experimental flower, the anthers were examined for contact and if contact had been made, the stigma was examined for deposition of self-pollen.

3. RESULTS

(a) Pollen export

Pollen-donor stigma treatment had a significant effect on the amount of pollen deposited on the stigmas of recipient flowers during hummingbird foraging bouts (analysis of variance (ANOVA) on log-transformed data, $p < 0.05$). Donors with closed stigmas exported a mean of 297.8 (s.e.m. = 61.4, $n = 22$) pollen grains to recipients, whereas donors with open (unmanipulated) and propped-open stigmas exported 126.1 (s.e.m. = 58.5, $n = 15$) and 64.9 (s.e.m. = 19.7, $n = 15$) grains, respectively (figure 3). The amount of pollen exported by closed-stigma donors was significantly greater than that of each of the other two pollen-donor treatments, but the latter two treatments did not differ significantly from each other (Fisher's protected least significant difference, $\alpha = 0.05$).

(b) Self-pollen deposition

Hummingbirds visiting flowers with glued-open stigmas deposited intrafloral self-pollen in only 7% of floral visits ($n = 68$). This could underestimate the proportion of stigmatic pollen loads containing intrafloral pollen because in some hummingbird visits the stigma is not touched, resulting in neither self- nor cross-pollen

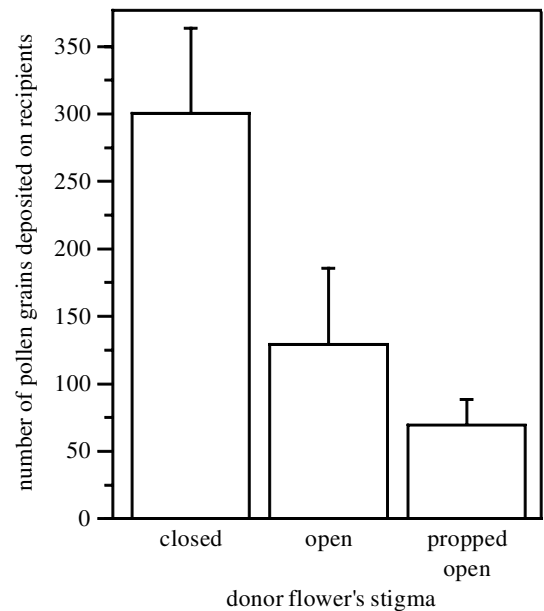


Figure 3. Mean (\pm s.e.m.) pollen loads exported to recipient flowers from pollen-donor flowers by hummingbirds foraging at artificial inflorescences. The effect of donor-stigma treatment on pollen export was significant (ANOVA on log-transformed data, $p < 0.05$).

receipt. In such visits there is no opportunity for stigma closure to reduce self-pollen deposition. In foraging visits to donor flowers with unmanipulated open stigmas (in the pollen-export experiment), hummingbirds contacted stigmas causing closure in 55% of visits ($n = 59$). Therefore, in the absence of stigma closure, self-pollen deposition would occur in *ca.* 13% of pollen-depositing visits (i.e. 7% out of the 55% of visits in which hummingbirds contact the stigma). It is unlikely that stigma closure is fully effective in eliminating even this relatively small amount of self-pollen deposition. In visits to unmanipulated donor flowers in which the stigma was readily discernible on the videotape, only one out of 12 stigmas contacted by hummingbirds was more than one-quarter closed before the hummingbird exited the flower. Often, the bird's head or upper bill was pressed against the open stigma while it drank nectar, preventing closure before retreat.

4. DISCUSSION

The results of this study indicate that herkogamy in the form of stigma closure is highly effective in reducing stigma interference with pollen export in the bush monkeyflower, and provide strong evidence that male–female interference can be an important selective force in floral evolution. Pollen-donor flowers with closed stigmas exported 2.4 times as much pollen as donors with open (unmanipulated) stigmas and 4.6 times as much pollen as donors with stigmas propped open to prevent closure. The mean pollen loads exported from all donor-flower treatments in the experiment fell within the range of pollen loads deposited on naturally pollinated flowers in the field (mean 338.8 grains, range 37–855 grains, $n = 39$; Fetscher 1999), indicating that the conditions in the export experiment reasonably reflected the flower–pollinator

interaction in nature. Seed production in the bush monkeyflower is an increasing function of pollen load up to ca. 650 grains (Fetscher & Kohn 1999). The mean pollen loads exported from all treatment groups were below this number and so the increase in pollen export conferred by stigma closure should correspond to an increase in seed paternity.

The benefit of stigma closure in terms of a reduction in intrafloral selfing, a phenomenon that should occur in, at most, only 13% of pollen-depositing visits to flowers whose stigmas were prevented from closing, was much less dramatic than the benefit of stigma closure in terms of the twofold difference in pollen export. The results of this study suggest that selection to decrease interference of the receptive stigma with pollen export has been a principle force in the evolution of stigma closure, and downplay the importance of avoidance of self-pollination as a selective force. The ability of stigma closure to reduce self-pollination relies on completion of closure within a pollinator's visit, such that the retreating pollinator cannot deposit self-pollen onto the open stigma. Videotaped hummingbird visits to flowers with open, unmanipulated stigmas revealed that, when the bird contacts the stigma, the bird's head is often pressed up against the open stigma while imbibing, preventing closure until the bird retreats. Therefore, stigma closure cannot be very effective in preventing self-pollen deposition within a visit. Conversely, the greatest amount of pollen is exported from a donor flower when the stigma is already closed before the bird arrives, and therefore pollen export does not rely on completion of stigma closure within a single visit by a pollinator. In view of this, it remains unclear why stigma closure in the monkeyflower is so rapid. Stigma closure has been attributed to the sudden loss of turgor of cells comprising the stigmatic tissue in response to touch (Linskens 1976). The speed of closure may be governed merely by physiological constraints and has not necessarily arisen as a result of direct selection for rapidity.

The closed-stigma treatment in the pollen-export experiment reflects the naturally occurring situation in which the flower has already been visited and the stigma has received some pollen (Fetscher & Kohn 1999). The permanent stigma closure typical of bush monkeyflowers receiving even subsaturating pollen loads may be adaptive because, once a certain amount of pollen has been received, it is more beneficial to switch to a male state and forgo any further potential fitness gains through female function because a flower with a closed stigma donates more pollen than a flower with an open stigma. In support of this interpretation, naturally pollinated flowers on intact plants whose stigmas were prevented from closing through experimental manipulation (as in figure 2*b*) received only slightly more pollen over their lifetime than did unmanipulated control flowers whose pollen typically arrives in a single visit (Fetscher & Kohn 1999). This suggests that, even in the absence of stigma closure, flowers would often receive only one pollen-depositing visit during their lifetime.

Approach herkogamy (*sensu* Webb & Lloyd 1986), in which the stigma is exerted beyond the position of the anthers, is the most commonly studied form of herkogamy and often correlates positively with the outcrossing rate

(Thomson & Stratton 1985; Holtsford & Ellstrand 1992; Belaoussoff & Shore 1995; Karron *et al.* 1997; Brunet & Eckert 1998; Motten & Stone 2000; Takebayashi & Delph 2000). The results of this study do not negate the importance of herkogamy as a selfing-prevention mechanism but rather illustrate that, at least in certain cases, reduction of male–female interference can be a highly potent selective force, perhaps even more so than selfing prevention. Clearly, demonstration that herkogamy affects the outcrossing rate is not sufficient evidence that selection on the mating system drives its evolution or maintenance. Future studies of the effects of variation in herkogamy should attempt to measure pollen export as well as the outcrossing rate.

In addition to herkogamy, other characters that have traditionally been interpreted as selfing-prevention mechanisms may also function, partially or primarily, as a means of reducing male–female interference. Moreover, the potential for male–female interference is not limited to that occurring within flowers; it can act between flowers within inflorescences. Harder *et al.* (2000) demonstrated in *Eichhornia paniculata* (Pontederiaceae) that female interference with male functions can take the form of interfloral deposition of self pollen on stigmas, leading to pollen discounting. They employed floral manipulations to show that dichogamy is effective in reducing the transfer of self-pollen between flowers within inflorescences, and hence male–female interference. Further support for the interference-reducing role of many floral characters comes from comparative data that show that herkogamy, dichogamy and monoecy (the separation of male and female organs into different flowers) often occur in plants that are self-incompatible (Lloyd & Webb 1986; Webb & Lloyd 1986). In fact, self-compatible species are no more likely to exhibit dichogamy than self-incompatible ones (Bertin 1993). These findings suggest that selection for outcrossing is insufficient to explain the incidence of dichogamy, herkogamy and monoecy, and some other factor, such as male–female interference, must also influence the evolution of these floral traits. Experiments and comparisons across diverse angiosperm species are needed to evaluate the relative importance of male–female interference and self-fertilization in the evolution of common floral traits.

I thank Josh Kohn, Nick Waser, Trevor Price, Gordon Fox, Debbie Balch, Jack Bradbury, Paul Dayton and two anonymous referees for valuable suggestions on the manuscript. I am grateful to Stacie Le, Natalie Wong and Shannon Rupert for excellent assistance in the field. This work was supported by a University of California Natural Reserves System Mildred E. Mathias Graduate Student Grant, the Explorer's Club and Sigma Xi.

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