

Beyond floricism: The pollination function of inflorescences

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Abstract

Mating by outcrossing plants depends on the frequency and quality of the interaction between pollen vectors and individual flowers. However, the historical focus of pollination biology on individual flowers (floricentrism) cannot produce a complete understanding of the role of pollination in plant mating because mating is an aggregate process, which depends on the reproductive outcomes of all of a plant's flowers. Simultaneous display of multiple flowers in an inflorescence increases a plant's attractiveness to pollinators, which should, in general, enhance mating opportunities. However, whenever pollinators visit multiple flowers on an inflorescence, self-pollination among flowers can reduce the pollen available for export to other plants (pollen discounting) and can increase the incidence of inbreeding depression for embryos and offspring. Therefore, the size of floral displays that maximize mating frequency and quality generally balance the benefits of attractiveness against the costs of self-pollination. This balance can shift considerably if different flowers serve female and male functions at one time (sexual segregation) and flowers are arranged in inflorescences so that pollinators visit female flowers before male flowers. However, the effectiveness of sexual segregation depends on the extent to which a particular inflorescence architecture induces consistent movement patterns by pollinators. In general, the consistency of pollinator movement patterns varies with inflorescence architecture and differs between pollinator types. Such variation creates many options for the evolution of the diverse inflorescence characteristics observed within angiosperms, which can be appreciated only by moving beyond a flor-centric perspective of the role of pollination in plant mating.

Keywords: floral display, geitonogamy, inflorescence architecture, mating, pollen export.

Received 27 February 2004; revision received 7 July 2004; accepted 7 July 2004

Introduction

The flower distinguishes angiosperms from other plants and its evolution contributed to the radiation of angiosperms into the dominant group of vascular plants (Dilcher 2000). The coordinated functioning of perianth, androecium and gynoecium allows flowers to enhance pollination either autonomously or through interaction with pollen vectors. Because of its functional and evolutionary significance, the flower has been the primary subject of reproductive botany, particularly studies of pollination. Indeed, pollination biology is sometimes referred to as anthecology (e.g. Baker 1983), combining

the Greek word for flower (anthos) with ecology and reflecting this flor-centric perspective.

Despite the flower being the essential organ of plant reproduction, mating is an aggregate process that depends on the reproductive outcomes of all of a plant's flowers. Whenever plants display multiple flowers simultaneously, these reproductive outcomes need not be independent, so that the floral display, rather than the individual flower, is the fundamental unit of plant mating. An interaction between a plant's flowers is most likely for flowers within the same inflorescence because they can act together to attract pollinators and their proximity increases the likelihood of flowers being visited by the same pollen vector. Joint visitation allows for self-pollination between flowers (geitonogamy) and for correlation in the quality and quantity of pollen export

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and import (see Harder & Barrett 1996). If inflorescence traits affect attraction and the incidence and consequences of joint visitation of flowers, then they will influence mating outcomes and be subject to natural and sexual selection.

Strangely, although inflorescence characteristics vary extensively within angiosperms (Troll 1964; Weberling 1989), their role in influencing pollination and plant mating has received little attention until recently (although see Parkin 1914; Burt 1965; Wyatt 1982). Even recent studies examining the influence of floral display size on pollinator attraction and geitonogamy (reviewed below) do not explore inflorescence function fully because they do not consider the reproductive consequences of inflorescence architecture. Such analysis is necessary for reproductive botany to move beyond floricism and to develop an inclusive understanding of plant mating.

In this paper we review experimental studies of the pollination function of inflorescences of animal-pollinated species and consider the implications for inflorescence evolution. We specifically focus on inflorescence traits that can affect pollinator behavior, namely the number and three-dimensional arrangement of flowers that are displayed simultaneously and the segregation of floral sex roles within the inflorescence. These display characteristics can differ from the aggregate characteristics of an inflorescence's total flower production. For example, *Eichhornia paniculata* (Pontederiaceae) plants produce several flowers on each inflorescence branch, such that typologically their inflorescences are panicles. However, typically only one flower is open on a branch, thus, the *E. paniculata* inflorescence functions as a raceme during pollination and not as a panicle. In such cases, total inflorescence characteristics must serve functions other than pollination, such as economic allocation of resources among flowers and fruits (see Stebbins 1973; Wyatt 1982; Schoen & Dubuc 1990), and are largely beyond the scope of this review. In considering the mating consequences of inflorescence display, we are interested both in the extent to which outcomes differ from those expected from examining flowers in isolation, and in new perspectives on the function of individual flowers that arise from recognizing the pollination function of inflorescences.

Why subdivide reproduction?

Most plants produce more than one large flower during a reproductive season, suggesting that multiple flowers enhance success as a female and/or male parent. This subdivision of reproduction involves two components. First, many plants display only a fraction of their flowers at once. Given a limit on daily resource availability, this temporal subdivision probably allows production of more flowers (and fruits) during the entire reproductive season

(Stebbins 1973). Sequential flower production also reduces the risk of insufficient pollination during unpredictable periods of pollinator scarcity (e.g. inclement weather). In addition, staggered flower presentation is the most effective mechanism for restricting pollen removal by individual pollinators. Such pollen packaging increases total pollen export when the proportion of pollen removed by individual pollinators that reaches stigmas varies negatively with the amount removed (Harder & Thomson 1989). Diminishing returns of this sort can result from pollinator grooming and layering of pollen on the pollinator's body (reviewed by Harder *et al.* 2001).

The second aspect of the subdivision of reproduction occurs when plants display multiple flowers simultaneously. At least two pollination benefits could arise from displaying more than one flower. Even slight separation of flowers within a display increases total display area, which should improve attractiveness to pollinators because an object's area determines the maximum distance from which it can be detected (reviewed by Dafni *et al.* 1997; Giurfa & Lehrer 2001). This enhancement of attractiveness appears to involve a trade-off between the number and size of flowers in a display, rather than a simple alteration in the number of flowers. For example, among species, nectar production per flower typically varies inversely with the number of open flowers (Harder & Cruzan 1990; Harder & Barrett 1992), so that a roughly equivalent expenditure of resources is partitioned among all open flowers. In addition to increasing attractiveness, simultaneous display of multiple flowers reduces pollen removal by individual pollinators, compared to a single large flower, because pollinators usually visit only a fraction of available flowers. As mentioned for staggered flowering, restriction of pollen removal enhances total pollen export, provided the display attracts enough pollinators that they eventually remove all pollen (Harder & Thomson 1989). Resolution of the conflicting functions of attracting many pollinators and restricting their behavior once they arrive is a recurring theme in the evolution of floral displays (Harder & Thomson 1989; de Jong *et al.* 1992; Iwasa *et al.* 1995; Harder & Barrett 1996).

Inflorescence size

Of all inflorescence characteristics, display size and its consequences for pollination and mating have received the most attention and have been the subject of recent detailed reviews (Harder & Barrett 1996; Snow *et al.* 1996; Harder *et al.* 2001). Thus, we will primarily summarize the features of general relevance to inflorescence function. The number of flowers displayed simultaneously affects two aspects of pollinator behavior, which directly influence the quantity and quality of plant mating: the number of pollinators attracted to a plant and the number of flow-

ers visited by individual pollinators. Within a plant population, large floral displays typically attract more pollinators than small displays (reviewed by Ohashi & Yahara 2001); however, attractiveness increases in a decelerating manner with display size (e.g. Harder & Barrett 1995). Individual pollinators visit more open flowers on large inflorescences than they visit on small inflorescences, but the proportion of flowers that they visit either does not differ or decreases with increasing display size within species (reviewed by Snow *et al.* 1996; Ohashi & Yahara 2001). Often the decline in the proportion of flowers visited by individual pollinators counterbalances the greater attractiveness of large inflorescences, so that the number of visits received by individual flowers varies little with display size (e.g. Harder *et al.* 2001; Karron *et al.* 2004). Given such a relationship, the characteristic size of a species' floral display cannot be understood by examining the pollination success of individual flowers in isolation.

The tendency of pollinators to visit multiple flowers within an inflorescence creates an opportunity for self-pollination among flowers (geitonogamy) provided the pollinators visit pollen-presenting flowers before those with receptive stigmas. Geitonogamy is probably a common feature of animal pollination for species with flowers that simultaneously donate and receive pollen. For example, the few studies that have measured self-pollination within and among flowers found that geitonogamy contributed over 40% of the self-pollination within inflorescences (Schoen & Lloyd 1992; Leclerc-Potvin & Ritland 1994; Eckert 2000; Karron *et al.* 2004). In general, the incidence of geitonogamy increases with display size (Crawford 1984; Harder & Barrett 1995; Snow *et al.* 1996; Brunet & Eckert 1998; Rademaker *et al.* 1999; Karron *et al.* 2004), as pollinators visit more flowers per inflorescence.

The self-pollination resulting from pollinators moving within inflorescences can have three detrimental consequences. First, because geitonogamy often involves the same pollinator behavior as pollen export, particularly when pollinators fly between flowers, pollen deposited geitonogamously tends to reduce the amount of pollen that could otherwise have been exported (pollen discounting, e.g. Harder & Barrett 1995). Second, in self-compatible species and those with late-acting incompatibility, self-pollination can reduce the number of ovules available for outcrossing (ovule discounting, e.g. Herlihy & Eckert 2002). Finally, given self-fertilization, inbreeding depression in self-fertilized embryos and offspring can reduce an individual's contribution to the next generation (reviewed by Charlesworth & Charlesworth 1987). Together, these consequences of geitonogamy should cause a plant that displays a large fraction of its flowers simultaneously to have lower reproductive output than a plant that displays fewer flowers at once and instead pre-

sents its flowers over a longer period. Therefore, selection on display size probably balances the attraction benefits of large displays with the limited costs of geitonogamy associated with small displays (de Jong *et al.* 1992; Harder & Barrett 1996).

Geitonogamy and its influence on optimal display size can be reduced or eliminated when the sex roles are segregated among different flowers (monoecy or dichogamy) or among different plants (dioecy). The effectiveness of sexual segregation within inflorescences in reducing geitonogamy depends on the extent to which pollinators visit functionally female flowers before functionally male flowers (hereafter female and male flowers). Reliable occurrence of such a visit sequence depends on a specific combination of pollinator and inflorescence characteristics: pollinators must follow a consistent route within inflorescences; and female flowers must occupy initial positions within this route, whereas male flowers must occupy terminal positions. For example, bumble bees (*Bombus* spp.) exhibit a strong tendency to begin visits to vertical inflorescences, such as racemes, on lower flowers and then move upward through the inflorescence, departing from upper flowers (Fig. 1a: also see Waddington & Heinrich 1979; Corbet *et al.* 1981; Rasheed & Harder 1997). This tendency to move upward appears to be a fixed behavior because it cannot be modified by altering the gradient of nectar per flower within racemes (Heinrich

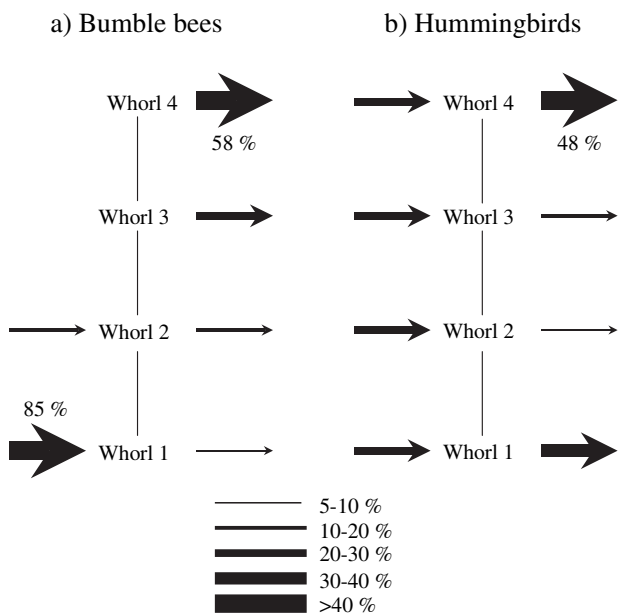


Fig. 1 Comparison of the positions of arrivals to and departures from 12-flowered racemes by (a) bumble bees (*Bombus huntii*, *Bombus impatiens* and *Bombus occidentalis*) and (b) rufous hummingbirds (*Selasphorus rufus*). Both panels depict the raceme in side-view (three flowers per whorl). Based on data from (a) Jordan (2000) and (b) Gross (2003).

1979). Presumably as an adaptive response to this stereotypic behavior, many racemose species visited by bumble bees present older, female flowers low in the display, with younger, male flowers presented above (reviewed by Bertin & Newman 1993). Indeed, this arrangement significantly reduces geitonogamous self-pollination and enhances pollen export compared to the presentation of either hermaphroditic flowers or female flowers above male flowers (Harder *et al.* 2000; also see Routley & Husband 2003). As a result, adaptive organization of sexual segregation within inflorescences should ease the constraints on the evolution of larger displays to enhance pollinator attraction.

Mass-flowering species, such as many animal-pollinated shrubs and trees, appear to contradict the expectation that the pollination and mating consequences of geitonogamy favor restriction of floral display size. The apparent paradox arises because a pollinator that visits a plant with hundreds or thousands of open flowers has an opportunity to visit so many flowers that most pollen should be dispersed geitonogamously, with little cross-pollination. To some extent, the proportion of pollen involved in geitonogamy can be reduced if stigmas of individual flowers remove only a small fraction of the pollen on pollinators' bodies (de Jong *et al.* 1992; Harder & Barrett 1996). However, the primary resolution of the paradox of mass flowering probably lies in the attraction of many pollinators by large displays (see Heinrich 1975; Stephenson & Thomas 1977; Augspurger 1980; Frankie *et al.* 1983; de Jong *et al.* 1992). As a consequence of this attractiveness, individual flowers will be depleted of nectar frequently and flowers with different visit histories will have accumulated different standing nectar volumes. In general, pollinators visit fewer flowers on displays with high versus low variance in nectar availability (Birnaskie *et al.* 2002). This response results because pollinators typically leave a plant after visiting a few empty flowers (e.g. Hodges 1985; Dreisig 1989; Cresswell 1990; Kadmon & Shmida 1992), so that visit sequences by individual pollinators can involve a very small fraction of the flowers displayed by intensively visited plants. For example, Augspurger (1980) found that bees visited an average of only 8.2 of the 226 flowers on *Hybanthus prunifolius* shrubs. Furthermore, the proportion of flowers visited declines strongly with mean display size for 17 plant species (Fig. 2). Such limited visitation of the available flowers in large displays by individual pollinators should limit geitonogamy and promote outcrossing provided the pollinators move between conspecific plants. However, the effectiveness of high variance in nectar availability as a mechanism for increasing pollinator movement between, rather than within, plants may vary during a plant's flowering period, as more pollinators include individual plants in their foraging routes. Stephenson (1982) attrib-

uted the peak in fruit set during the final phase of flowering in *Catalpa speciosa* trees to such a change in visitation intensity per flower. Unfortunately the hypothesis that attraction of many pollinators by mass displays reduces the number of flowers visited by individual pollinators remains largely untested because few studies of mass-flowering species have reported relevant aspects of pollinator behavior (note the paucity of examples with >50 flowers in Fig. 2).

Inflorescence architecture

The extensive diversity of inflorescence architecture (e.g. Troll 1964; Weberling 1989) demands explanation; however, the function of display architecture has received almost no experimental analysis. If display architecture affects mating outcomes, then it must do so by influencing pollinator behavior. The preceding review of the consequences of display size and sexual segregation for pollination leads to parallel expectations that display architecture affects three aspects of pollinator behavior that could affect pollination and mating: pollinator attraction, the number of flowers visited and the consistency of movement patterns within inflorescences.

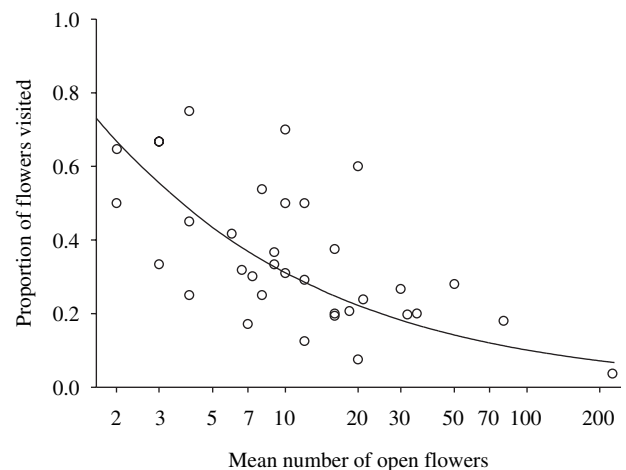


Fig. 2 Relationship between mean floral display size and the average proportion of flowers visited by pollinators of 17 plant species, with multiple observations for some species. Data were collected from the literature (Pyke 1978; Augspurger 1980; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer *et al.* 1989; Pleasants & Zimmerman 1990; Barrett *et al.* 1994; Robertson & Macnair 1995; Brody & Mitchell 1997; Goulson *et al.* 1998; Ohashi & Yahara 1998; Johnson & Nilsson 1999; Vrieling *et al.* 1999; Galloway *et al.* 2002; Ohashi 2002; Mitchell *et al.* 2004). The regression line is based on an analysis that considered the dependence of $\ln(\text{number of flowers visited})$ on $\ln(\text{floral display size})$ and accounted for the repeated measurement of individual species by single studies ($F_{1,24.5} = 76.26$, $P < 0.001$). Note the logarithmic scale for display size.

The consequences of display architecture for pollinator attraction appear almost completely unexplored. Fishbein and Venable (1996) manipulated the floral displays of *Asclepias tuberosa* and found that an intermediate density of flowers attracted the most pollinators (primarily *Apis mellifera*). Gross (2003) presented free-foraging rufous hummingbirds (*Selasphorus rufus*) with mixed arrays of artificial, 12-flowered racemes, panicles and umbels. Although birds visited umbels more quickly, because of the higher density of flowers, they exhibited no preference for any of the three inflorescence types. We know of no other studies that have considered the consequences of display architecture for pollinator attraction.

Display architecture can affect the number of flowers visited by individual pollinators. Hainsworth *et al.* (1983) found that hummingbirds presented with arrays of 15 artificial flowers visited approximately 13 flowers on vertical one-dimensional arrays, between 9–10 flowers on vertical two-dimensional arrays, and between six and seven flowers on three-dimensional hemispheric arrays. Interestingly, birds revisited both a smaller number and smaller proportion of flowers on three-dimensional arrays than on simpler arrays (also see Pyke 1981). These results demonstrate that dimensional complexity affects the behavior of individual pollinators on inflorescences. However, most architectures differ in the three-dimensional arrangement of flowers, rather than in the number of dimensions, so the relevance of these results for pollination and mating is not clear.

Two studies present direct evidence that differences in the three-dimensional arrangement of flowers affect pollinator behavior. Jordan (2000) and Gross (2003) assessed the responses of bumble bees and rufous hummingbirds, respectively, to artificial racemes, panicles and umbels with 12 artificial flowers containing fixed nectar volumes. Both bumble bees and hummingbirds visited significantly more flowers on umbels than on panicles, on average, but the difference involved only a single additional visit. The dominant influence of display architecture on pollinator behavior in these experiments involved the consistency of routes that pollinators followed among flowers within inflorescences. For example, in contrast to the typical upward foraging used by bumble bees while visiting racemes (Fig. 3a), Jordan (unpubl. data, 2000) found that bumble bees followed much less consistent routes on artificial panicles (Fig. 3b) and even less consistent routes on umbels (Fig. 3c: see Giurfa & Núñez 1993 for similar behavior on capitula). Of particular interest is the greater frequency of downward movements on panicles than on racemes. Branches augment the breadth of panicles, so that bees can move downward while also moving laterally. This opportunity for more 'diagonal' movement may relax the constraint that induces upward movement on more vertical inflorescences, such as racemes.

The experiments of Jordan (2000) and Gross (2003) may underestimate the effect of inflorescence architecture on the number of flowers visited by pollinators under more natural conditions, when visit history affects nectar volumes. For example, bumble bees leave vertical inflorescences after visiting a single empty flower (Hodges 1985; Dreisig 1989), whereas they must encounter several empty flowers before they leave panicles (Kadmon & Shmida 1992) or head-like inflorescences (Cresswell 1990). The relatively consistent foraging paths of bumble bees on racemes (Fig. 3a) will tend to create a strong correlation in the standing crop of nectar between adjacent flowers after a bee's visit. As a result, a subsequent bee can use the nectar volume in a single flower on a raceme as an indicator of whether moving to the next flower or leaving the inflorescence would be more profitable. In contrast, because bees follow less consistent foraging paths on panicles and umbels, the standing crop of nectar will be less correlated among adjacent flowers, so that visits to several flowers will be required to assess the nectar availability on the entire inflorescence. Therefore, under natural conditions, pollinators probably visit fewer flowers on inflorescence architectures that promote consistent foraging paths than on architectures of equal size on which pollinators move less predictably.

The differences in pollinator behavior on contrasting inflorescence architectures are likely to affect plant mating in a complex manner. To investigate these effects, Jordan (2000) simulated pollen dispersal based on the bee behavior that he observed in his experiments with artificial racemes, panicles and umbels. When all flowers within inflorescences functioned simultaneously as pollen recipients and donors, umbels experienced 10% more self-pollination and exported 7% more pollen than panicles after a visit by a single bee, with racemes falling between these extremes. This positive association between self-pollination and pollen export appears to contradict the expectation that geitonogamy reduces the pollen available for export. However, two factors differed as a result of a bee visiting one more flower on umbels than on panicles. First, the extra transition between flowers on umbels increased geitonogamy and pollen discounting. Second, the visit to an extra flower also contributed more pollen to the pollinator's body, despite pollen discounting, thereby increasing the pollen available for export. This positive association between self-pollination and pollen export would not have persisted if plants had received visits from enough pollinators to remove all of their pollen.

The differences in consistency of pollinator movement among inflorescence architectures (Fig. 3) should be particularly significant for the mating of plants in which the sex roles are segregated among different flowers (monoecy and dichogamy). To explore this possibility, Jordan

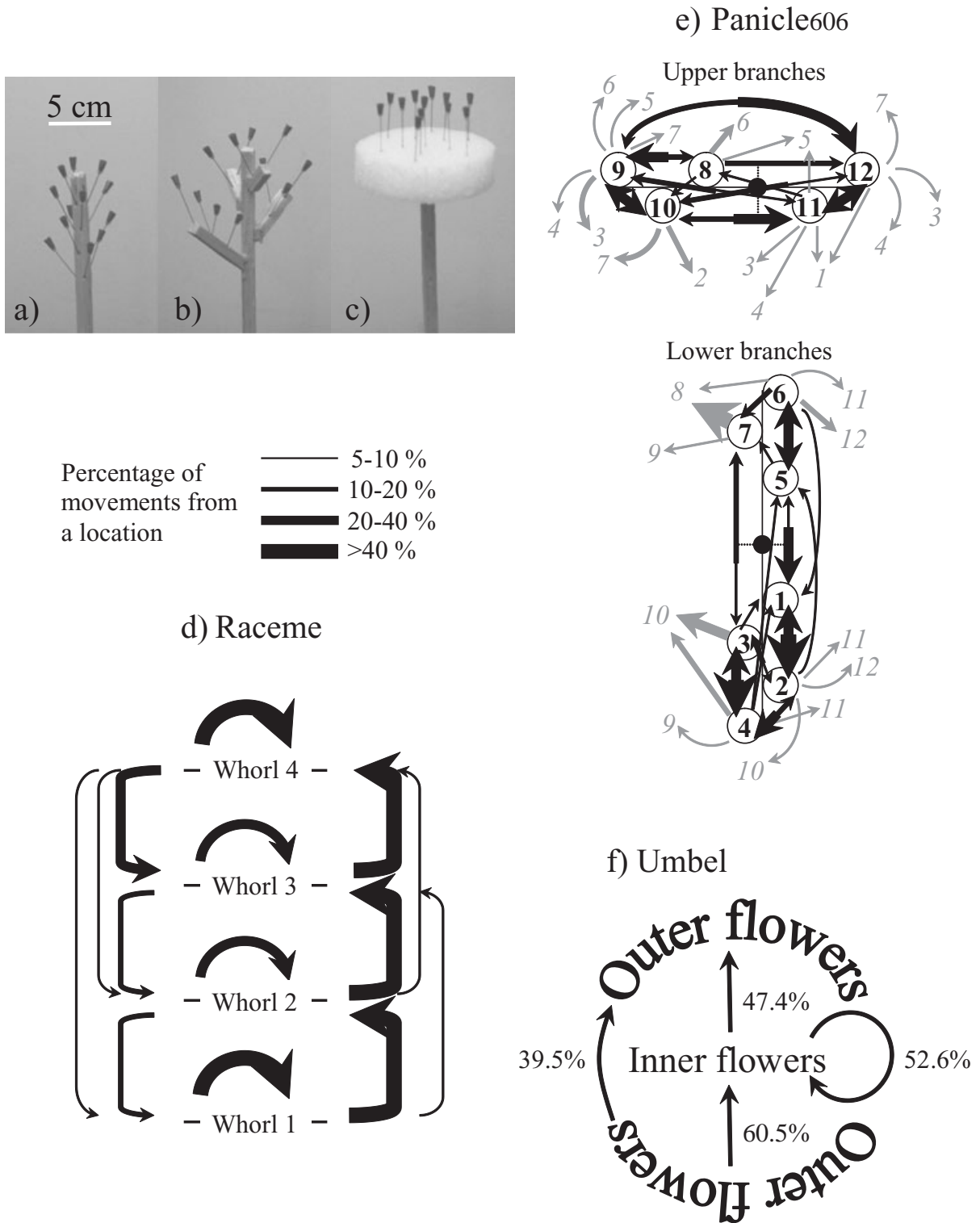


Fig. 3 Photographs of the artificial (a) racemes, (b) panicles and (c) umbels used by Jordan (2000) to examine the influences of inflorescence architecture on foraging by bumble bees (*Bombus huntii*, *Bombus impatiens* and *Bombus occidentalis*) and summaries of the proportions of movements from individual flowers to other flowers for these three architectures (panels d, e and f, respectively). Panel (d) depicts the side-view of a raceme with three flowers per whorl. Panel (e) depicts the top-view of a panicle, with numbers indicating specific flower positions and the black spot representing the main stem. Panel (f) illustrates the top-view of an umbel, which had six outer and six inner flowers.

(2000) simulated pollen dispersal with six of the 12 flowers in inflorescences only receiving pollen (female flowers) and the remainder only donating pollen (male flowers). Female flowers were assigned to the six positions on a specific architecture at which bees began inflorescence visits most often, whereas male flowers occupied the remaining six positions. Sexual segregation reduced self-pollination by 30–80%, with the strongest effect for racemes and the weakest for umbels. This reduction in self-pollination was accompanied by enhanced pollen export (after accounting for differences in the number of pollen-presenting flowers). These differences resulted because bees were much more likely to move from male to female flowers on umbels than on racemes, with panicles being intermediate. This difference in the consistency of bee movement patterns would allow sexual segregation to limit geitonogamy on racemes more effectively than the less consistent routes followed by bees on panicles and, in particular, umbels.

Jordan's (2000) simulations suggest that particular combinations of inflorescence architecture and sexual segregation should be expected for specific pollinator types. The particular advantages of racemes in this context may explain the prevalence of this architecture among plants pollinated by large-bodied bees and the relative rarity of umbels. Some species pollinated by large-bodied bees do produce umbels; however, many of these species exhibit synchronous protandry, whereby all flowers in the inflorescence open simultaneously and proceed together through male and then female phases (e.g. Aizen 2001; Bhardwaj & Eckert 2001). Such a flowering pattern necessarily eliminates self-pollination and its mating costs (Harder & Aizen 2004) and may be implemented relatively easily in umbels, given the common origin of flower pedicels.

An obvious corollary to the predicted association between pollinator types and inflorescence architectures is that differences between pollinators in movement patterns should favor contrasting inflorescence characteristics. This expectation is clearly illustrated by a comparison of Jordan's (2000) observations of bumble bees and Gross's (2003) observations of hummingbirds feeding on artificial racemes (Fig. 1). In contrast to the bottom-up foraging pattern of bumble bees (Fig. 1a), hummingbirds begin visits to racemes indiscriminately with respect to position and move up or down with roughly equal frequency, departing from either top or bottom flowers (Fig. 1b; also see Wolf & Hainsworth 1986). Clearly, presentation of female flowers below male flowers on a raceme would be less effective in reducing geitonogamy during hummingbird visits than during bee visits. Given that hummingbird pollination in North American flora typically evolved within bee-pollinated lineages (Grant & Grant 1968), it appears likely that such transitions involv-

ing ancestral, racemose species induced changes in either inflorescence architecture or the organization of sexual segregation within the inflorescence.

For example, most *Delphinium* species are pollinated by large-bodied bees and have vertical racemes. In these bee-pollinated species, floral development proceeds acropetally and flowers are protandrous, so that inflorescences typically present older, female-phase flowers below younger, male-phase flowers (e.g. Fig. 4a). In contrast, a hummingbird-pollinated species, *Delphinium cardinale*, has similar inflorescence architecture, but flowers on the main raceme open simultaneously. Given protandrous floral development, this synchrony results in an inflorescence with either female- or male-phase flowers (Grant & Grant 1968). Although the separation of sex roles resulting from this pattern of floral development breaks down somewhat when small, lower inflorescence branches begin flowering (Fig. 4b), it should greatly reduce geitonogamy during visits by hummingbirds with inconsistent movement patterns. This example illustrates that differences among pollinators in their movement patterns may select for contrasting inflorescence characteristics, thereby contributing to some of the diversity in floral displays observed within angiosperms.

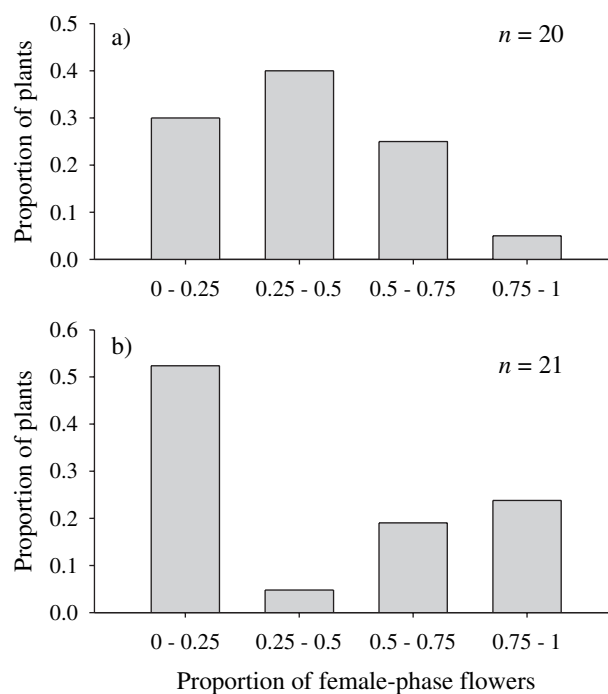


Fig. 4 Comparison of the frequencies of female- and male-phase flowers in inflorescences of (a) bee-pollinated *Delphinium stachydeum* and (b) hummingbird-pollinated *Delphinium cardinale*. Data collected in the Santa Rosa Mountains, Nevada (*D. stachydeum*) and at Santa Barbara, California (*D. cardinale*) by W. E. Gross (unpubl. data, 2000).

Relationship between inflorescence and floral characteristics

The preceding review clearly illustrates that flowers do not act independently to determine plant mating whenever plants display multiple flowers simultaneously. As a result, floral evolution must occur within the mating consequences for the entire display. Similarly, inflorescence evolution must depend on the characteristics of the component flowers. We now briefly consider three examples of the consequences of this reciprocal dependence for the evolution of reproductive traits.

Selection of display size

We have proposed that a species' floral display size is an adaptation that balances the benefits of attraction against the costs arising from geitonogamy. However, display size is not an intrinsic, unitary trait that can be selected independently. Instead, display size arises from the aggregate phenology of individual flowers (Ishii & Sakai 2001; Meagher & Delph 2001) and is determined by the relative rates at which flowers open and wilt. As a result, selection can alter display size only by affecting anthesis rate and/or floral longevity. Correspondingly, the scope for selection to alter these floral traits depends on the mating consequences associated with changes in display size (e.g. Schoen & Ashman 1995). Clearly, complete understanding of floral and display dynamics requires recognition that flowers do not function in isolation and that display size is an aggregate trait.

Our review of display size implied that this size is a fixed adaptation. However, optimal display size depends on pollinator abundance (Harder & Barrett 1996), which can vary considerably within and between flowering seasons and among populations. In such cases, adjustment of display size in response to the prevailing pollinator abundance would be advantageous. The aggregate nature of floral displays allows for such flexibility when floral longevity varies negatively with the rate of pollen receipt, which is the case for many angiosperm species (van Doorn 1997). In such species, infrequent pollination extends floral longevity, so that the anthesis of new flowers combined with the persistence of older flowers results in a larger floral display. In contrast, when pollinators visit frequently, pollinated flowers senesce quickly, resulting in a smaller display comprised mainly of young flowers (Karrenberg & Jensen 2000; L. D. Harder & S. D. Johnson, unpubl. data, 2001). This facultative response of display size to pollinator abundance allows for greater attractiveness when pollinators visit rarely, and reduced geitonogamy when pollinators visit frequently (L. D. Harder & S. D. Johnson, unpubl. data, 2001). Because of these contrasting benefits, selection on display size should

often result in the evolution of floral mechanisms that allow adjustment of display size in response to a plant's recent pollination history.

Dichogamy as a floral and inflorescence mechanism

Our discussion of sexual segregation focused on its role in reducing geitonogamy and associated pollen discounting. One form of segregation, dichogamy, also reduces intrafloral self-pollination and could enhance pollen export of individual perfect flowers through temporal separation of pollen presentation and stigma receptivity (reviewed by Lloyd & Webb 1986; Bertin & Newman 1993; although see Galloway *et al.* 2002). This ability of dichogamy to serve both floral and inflorescence functions raises questions concerning the relative importance of these roles (Routley & Husband 2003).

The importance of dichogamy as a mechanism reducing intrafloral versus geitonogamous self-pollination probably varies with floral display size (Routley & Husband 2003). In small displays, pollinators necessarily visit few flowers. In this situation dichogamy must primarily reduce interference between sex organs *within* flowers, including intrafloral self-pollination. Larger displays allow pollinators to visit more flowers per inflorescence, thereby enhancing the opportunity for geitonogamy and associated pollen discounting. By counteracting this opportunity, dichogamy becomes more important as a means of reducing negative interaction *between* flowers. Therefore, the primary function of dichogamy probably depends on the pollination context established by inflorescence display size. This functional diversity can be appreciated only when the roles of dichogamy are viewed within the context of the entire inflorescence.

Sex allocation within inflorescences

Flowers within inflorescences can experience different pollination environments depending on when they open during their inflorescence's blooming period and where they are located within the display. As a result, flowers within an inflorescence can differ in their ability to function as female and male organs. If this heterogeneity in performance occurs predictably within inflorescences, then selection should modify allocation to female versus male function among flowers to enhance a plant's mating performance (see Brunet & Charlesworth 1995).

For species with staggered anthesis of flowers that live several days, display size changes from small initially, to maximal during peak flowering, and then to small again as only the final flowers remain (e.g. Ishii & Sakai 2002). Given the positive relationship between pollinator attraction and display size, the rate of pollinator visitation to initial flowers probably increases during their lives as

they participate in a growing display, whereas final flowers probably experience declining visitation as display size declines. Given such a temporal pattern in visitation rate, initial flowers of a protandrous species will have limited opportunity for pollen export during their initial male phase, but better prospects for pollen import during their later female phase (e.g. Ishii & Sakai 2002). In contrast, final flowers will receive more pollinator visits during the male phase than during the female phase. This shift in performance should favor ovule-biased investment in initial flowers and pollen-biased investment in final flowers of protandrous species.

Position within a floral display can also affect a flower's relative female versus male success. For example, Barrett *et al.* (1994) found threefold more self-pollination in upper flowers of vertical *Eichhornia paniculata* inflorescences than in lower flowers, as a result of the upward movement of bee pollinators (also see Rademaker *et al.* 1999). Self-pollination in this experiment significantly reduced the pollen available for export (Harder & Barrett 1995), so that lower flowers probably imported more outcross pollen, but exported less pollen, than upper flowers. Such a pattern would favor greater ovule production in lower flowers and greater pollen production in upper flowers, particularly in species with a high genetic load (Brunet & Charlesworth 1995).

In general, the scope for selection of position-dependent sex allocation will depend on the variances in self-pollination, pollen import and pollen export among flowers within inflorescences. These pollination variances should be accentuated when pollinators follow consistent paths among flowers within inflorescences. As we have already demonstrated, such consistency differs among pollinators and inflorescence architectures. For pollinators that follow consistent paths (e.g. upward movement on vertical inflorescences), Barrett *et al.* (1994) demonstrated that among-flower variance in self-pollination depends on the specific combination of the number of flowers that each pollinator visits (a function of display size) and the proportion of the pollen on a pollinator's body removed by each stigma (a floral trait). Pollination variances will also fluctuate with overlap in the flowering periods of individual flowers. In species with distinct cohorts of flowers (e.g. displays of 1-day flowers), individual flowers have a fixed relative position within the display (e.g. bottom vs top), which fosters variance in female and male performance among flowers. In contrast, in species with staggered anthesis of long-lived flowers, a flower's relative position in the display can change as the wave of flowering progresses through the inflorescence. Such a pattern will tend to equalize female and male performance among flowers within an inflorescence and reduce the opportunity for selection on heterogeneous sex allocation among flowers.

The preceding hypotheses predict higher pollen : ovule ratios in flowers produced later in an inflorescence's blooming period and higher on vertical inflorescences. Similar patterns could result from declining resource availability during a plant's flowering period and/or reduced vasculature to distal flowers (reviewed by Diggle 1995). However, the predicted variation in pollen : ovule ratios has been observed in eight liliaceous species (Thomson 1989; Nishikawa 1998) and a spring-ephemeral *Corydalis* (Kudo *et al.* 2001) in which flowers are preformed during the preceding growing period. In addition, in several of the species studied by Thomson (1989) the flowers that opened first exhibited lower pollen : ovule ratios, despite occupying more distal positions in the inflorescence. These results are more consistent with selection of sex-allocation patterns that enhance mating success, than with either resource competition among flowers or positional constraints on resource distribution. Thus, it appears likely that variation in the pollination environment among flowers within inflorescences shapes the evolution of sex allocation.

Concluding comment

This review illustrates that pollination biology is undergoing a shift in perspective from the historical flor-centric emphasis to an expanded view that considers the function of a plant's entire display. This evolving perspective enhances understanding of many recognized floral traits (e.g. dichogamy, floral longevity) and identifies inflorescence traits as subjects of interest in their own right (e.g. architecture, variation in sex allocation). This broadening of perspective has been accompanied by increased integration of ecological studies of pollination with more genetic studies of plant mating (see Harder & Barrett 1996; Holsinger 1996; Morgan & Schoen 1997). These developments hold considerable promise for progress in understanding the diversity of floral design and display among angiosperms.

Acknowledgments

We thank the organizers of the Society for the Study of Species Biology symposium on Diversity of Reproductive Systems in Plants: Ecology, Evolution and Conservation for the opportunity to compile this review of floral display and J. C. Vamosi for comments on the manuscript. The Natural Sciences and Engineering Research Council of Canada funded this research.

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