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The effects of floral design and display on pollinator economics and pollen dispersal

Animal pollination is a mixed blessing for angiosperms. Animals carry pollen readily because they are mobile and large relative to pollen grains. Furthermore, animals learn to associate floral signals with the presence of food and so move between conspecific plants relatively consistently (Chittka *et al.*, this volume; Gegear & Laverty, this volume; Giurfa, this volume; Menzel, this volume). However, animals act in their own interests, which often conflict with successful pollen transport (e.g., only about 1% of a plant's pollen production reaches stigmas; Harder 2000). Consequently, manipulation of pollinator behavior to promote cross-pollination is a prevailing theme in the evolution of floral design (form, color, nectar, and fragrance production) and display (inflorescence size and architecture).

10%
Pollen
reaches
Stigma

This chapter reviews three aspects of pollinator manipulation by plants and their effects on pollen dispersal. First, because pollen dispersal for most animal-pollinated plants depends on the general responses of feeding pollinators to their foraging environment, we consider the underlying economic principles that establish the opportunities for floral manipulation. Second, we outline influences on the typical pattern of pollen dispersal among flowers for plants with granular pollen, and summarize how flower design affects this pattern (for a review of dispersal of orchid pollen, see Harder 2000). Finally, because pollination and mating success are characteristics of entire plants, rather than individual flowers, we consider how floral display affects pollinator attraction and within-plant behavior to determine pollen dispersal.

Pollinator economics

Most pollinators visit flowers to gather food. In general, foraging involves economic principles whereby a resource's utility depends ultimately on

its relative contribution to the forager's fitness. However, animals probably cannot evaluate the fitness consequences of different foraging options; rather, they must assess opportunities based on the proximate benefits and costs associated with current physiological and ecological conditions. Often, the behavior of experienced feeding animals maximizes a single variable, or foraging currency, that integrates foraging benefits and costs (Stephens & Krebs 1986). Such behavior bears diverse consequences for pollination, because it affects a pollinator's choice of plant species (e.g., Rasheed & Harder 1997a), choice of individual plants (e.g., Heinrich 1979; Waser & Price 1983; Thomson 1988), and behavior on those plants (e.g., Galen & Plowright 1985; Hodges 1985; Rasheed & Harder 1997b).

Foraging pollinators typically visit flowers for nectar and/or pollen; these resources differ distinctly with respect to both foraging benefits and costs. Most pollinators visit flowers for the concentrated, easily digested energy in nectar. Because animals ingest nectar, they can readily determine their intake rate and whether a flower is empty (e.g., Dreisig 1989). The main handling cost of nectar collection involves the time and energy required to drink nectar from flowers. This cost depends primarily on the volume of nectar ingested, its depth within a flower, the animal's body size, and the length of its proboscis (see Montgomerie 1984; Harder 1986). Consequently, the choice of plants within and between plant species varies with pollinator size and morphology (e.g., Harder 1985, 1988). Furthermore, because the rate of flower manipulation increases with experience, foraging decisions can depend on an individual pollinator's learning ability (Gegear & Lavery, this volume).

Unlike nectar, pollen offers a rich source of protein, amino acids, lipids, and sterols, compared to most other plant tissues (Stanley & Linskens 1974). However, pollen use requires specific collecting and digestive abilities, given the small quantities of pollen available in individual flowers and the indigestibility of pollen exine. Consequently, only some pollinators (primarily non-parasitic bees, syrphid flies, and masarine wasps) satisfy their protein needs by feeding from flowers. Instead of ingesting pollen directly from anthers, most of these animals harvest it in three steps: (1) external removal on the animal's body; (2) grooming; and (3) either consumption or transfer to specialized, external carrying structures (scopae, including corbiculae) for transport to a nest (Holloway 1976; Michener *et al.* 1978; Thorp 1979). The removal step can be cost-free if it occurs passively during nectar collection, or it can require considerable

effort, as when bees contract their flight muscles rapidly to buzz pollen from poricidal anthers (reviewed by Buchmann 1983; also see Harder & Barclay 1994; King & Buchmann 1996). Grooming also elevates the cost of pollen collection relative to nectar collection, especially because it typically occurs during flight (Holloway 1976; Harder 1990a; Michener *et al.* 1978), which increases metabolic effort 10-fold (Ellington *et al.* 1990). Even though most bees carry pollen externally, they detect variation in the amount and quality of pollen removed from individual flowers (Cane & Payne 1988; Buchmann & Cane 1989; Harder 1990a; Robertson *et al.* 1999), perhaps by setae on the scopae that are coupled to displacement sensors (Ford *et al.* 1981) or by assessment of grooming effort. In response to such variation, bees alter their behavior to promote pollen-collection profits (Rasheed & Harder 1997a, b). This behavior often results in individual bees not depleting flowers of pollen, even when they visit for no other resource (Harder 1990b; Harder & Barclay 1994).

In addition to handling costs, the relevant foraging currency must incorporate the time and energy expended on other activities. These additional costs always include travel within and between plants. For animals that visit flowers to provision offspring, transit costs between nests and foraging sites are also relevant, so that foraging costs equal the total expense of foraging. In contrast, pollinators that visit flowers to sustain other activities, such as defending a territory, finding mates, or searching out oviposition sites, must accommodate the additional costs associated with these activities (Montgomerie *et al.* 1984; Houston & Krakauer 1993).

Given the benefits (B), time costs (T), and energy costs (E) of nectar and pollen collection, what currencies do pollinators typically maximize? The behavior of nectar feeders usually maximizes either net intake rate ($[B-E]/T$; Hodges 1981; Gass & Roberts 1992; Hainsworth & Hamill 1993) or net foraging efficiency ($[B-E]/E$; Schmid-Hempel & Schmid-Hempel 1987; Tamm 1989), whereas that of pollen feeders maximizes gross efficiency (B/E ; Rasheed & Harder 1997a, b). Maximization of foraging rate maximizes daily gains for animals that forage to satisfy their own needs, whereas animals that maximize efficiency while provisioning other individuals maximize the overall daily delivery of resources to their nests (Ydenberg *et al.* 1994). In addition, a provisioning forager that maximizes its foraging efficiency promotes its reproductive output when the chance of mortality increases with foraging effort (Houston *et al.* 1988). In general, energy costs influence efficiency more than rate, so that when pollinators maximize efficiency they limit expensive behaviors, especially

flight. As a result, maximizing efficiency rather than rate requires pollinators to visit more flowers per inflorescence (Rasheed & Harder 1997b) and to work each flower longer. As we discuss below, both of these behavioral responses affect pollination, so that foraging currency will affect plant mating.

Most studies of the currencies that motivate pollinator behavior have considered animals feeding exclusively on either nectar or pollen. However, animals that rely on flowers for both energy and protein require a balanced diet of nectar and pollen for adequate nutrition (e.g., Haslett 1989; Camazine 1993; Plowright *et al.* 1993). To maintain this balance, flower-dependent animals may need to compromise the economic collection of either resource to optimize overall diet composition. Such compromises may be common, because flower-dependent animals often collect nectar and pollen from different plant species (Brian 1957; Liu *et al.* 1975; Teräs 1985) that differ in their relative availability of these resources. N.M. Williams and V.J. Tepedino (unpublished manuscript) proposed that, in such circumstances, solitary bees minimize the total time spent collecting all the pollen and nectar required to provision a single offspring. Given relatively constant mass and quality of offspring provisions, such behavior would maximize the gross rate of resource collection per provision. Williams and Tepedino observed that female *Osmia lignaria* (Megachilidae) divided their foraging effort between a rich nectar source (*Hydrophyllum capitatum*) and a rich pollen source (*Salix* spp.) in proportions expected from time minimization, even though these species were separated by 300 m. In contrast to solitary bees, social bees need not always compromise economic collection of nectar and pollen, because they can achieve a balanced input by varying the proportions of dedicated pollen- and nectar-foragers (Brian 1952; Cartar 1992; Camazine 1993; Plowright *et al.* 1993).

If a pollinator is to maximize some benefit–cost ratio between the beginnings of consecutive foraging bouts, how should it decide whether to continue its current behavior, such as a flower visit, or switch to a different behavior? Quite simply, an individual act serves the longer-term goal of currency maximization as long as its instantaneous benefit–cost ratio (i.e., marginal value) exceeds the average ratio expected by ending the current behavior and beginning anew (marginal value theorem: Charnov 1976). This principle underlies many aspects of pollinator behavior, including: whether to deplete individual flowers of nectar and/or pollen (Hodges & Wolf 1981); whether to move to another flower on the same plant, or to another plant (Pyke 1979; Hodges 1985; Kadmon & Shmida

1992; Rasheed & Harder 1997*b*); whether to move to a neighboring, or more distant plant (Cibula & Zimmerman 1984); whether to start feeding on a different plant species (Zimmerman 1981); and when to end a foraging bout and either return to the nest or transfer to another behavior (Schmid-Hempel *et al.* 1985). Three features of the involvement of a benefit–cost ratio in these decisions warrant notice. First, as will become apparent below, all of these behaviors influence the pattern of pollen dispersal, so that foraging currency defines the linkage between many floral characteristics and pollination success. Second, the consequences of a floral characteristic, such as nectar volume or concentration, for pollinator behavior depends on its influence on the relevant foraging currency, rather than its effects on benefits or costs alone (e.g., Harder & Real 1987). Finally, because the value of a particular behavior to a pollinator depends on the average currency in the environment, the details of pollinator behavior (and the associated pollination) are often context dependent (e.g., Harder & Barrett 1996; Kunin 1997; Smithson & Macnair 1997).

Notwithstanding the widespread occurrence of currency maximization by pollinators, some solitary bees restrict their pollen collection (but not necessarily nectar collection) to a few related plant species even when other species seemingly offer greater rewards (reviewed by Wcislo & Cane 1986). Based on the limited available data, such specialization seems to be genetically determined (Thorp 1969; Williams 1999). This innate specialization is sometimes associated with behavioral and morphological adaptations for harvesting resources from particular plant taxa, which may increase pollination effectiveness. Innate specialization can benefit pollination by promoting pollen transfer between conspecific plants, although in this respect it does not differ fundamentally from short-term specialization by a generalist pollinator that maximizes its current foraging returns (see Waser 1986). On the other hand, adaptations for collecting pollen from specific plant species can impair pollination if they enable pollen specialists to function more as pollen thieves than as pollinators (e.g., Eickwort 1967; Cane & Buchmann 1989; Williams & Thomson 2001).

Flowers and pollen dispersal by individual pollinators

Individual flowers serve pollination by contributing to a plant's overall attractiveness to pollinators (including both signaling and energetics) and by controlling the transfer of pollen to and from each visitor. Because attraction typically involves all flowers open on a plant, we review this function when we discuss inflorescences (below). Here, we consider the

role of individual flowers in controlling pollen exchange with pollinators. Floral characteristics mediate this exchange by determining which areas of pollinators' bodies contact a flower's pollen and stigma(s), and the intensity and duration of that contact. Most aspects of floral form, as well as the production of nectar and floral oils, contribute to these pollination functions. Before addressing the roles of specific floral features in pollen export and import, we review the general pattern of pollen dispersal by a single pollinator from a specific donor flower to recipient flowers.

For most angiosperms, individual pollinators transport donor pollen to several or many recipient flowers (reviewed by Morris *et al.* 1994; Harder & Wilson 1998), because each stigma receives only a fraction of the pollen carried by a pollinator from a specific donor flower. In general, successive recipient flowers receive progressively less pollen from a particular donor (see Fig. 15.1a) due to deposition on stigmas and transport losses (e.g., grooming). If the pollen carried by a pollinator behaved as a single, completely mixed population, receipt of donor pollen by successive recipient flowers would decline as expected for simple geometric decay – as in Fig. 15.1a. However, in reality the decline is more rapid among initial recipients and more gradual among later recipients (reviewed by Morris *et al.* 1994), suggesting that the pollen carried by a pollinator behaves as a subdivided population with heterogeneous transport conditions.

Such subdivision could arise either passively or actively (Harder & Wilson 1998). Passive segregation could arise through at least three mechanisms: differences in the ability of areas on a pollinator's body to carry pollen (e.g., hairy head versus smooth mouthparts); variation in the incidence and intensity of contact by pollinators with anthers and/or stigmas; and accumulation of pollen in layers on the pollinator. Active segregation of pollen on a pollinator arises from behaviors such as grooming or movements of the mouthparts. These behaviors affect pollen on some sites on a pollinator's body (exposed sites), but not on others (safe sites: e.g., Kimsey 1984; Thomson 1986). Such behaviors could also move pollen from exposed to safe sites, supplementing safe sites with pollen from flowers visited previously while depleting exposed sites. As a result, the proportion of pollen from a specific donor flower that is dispersed to stigmas via safe versus exposed sites increases steadily as the pollinator visits successive recipient flowers.

Variation in pollen removal from a donor flower by individual pollinators is modified by grooming and layering dynamics so that pollen export increases non-linearly as removal increases (Harder & Wilson 1997). When

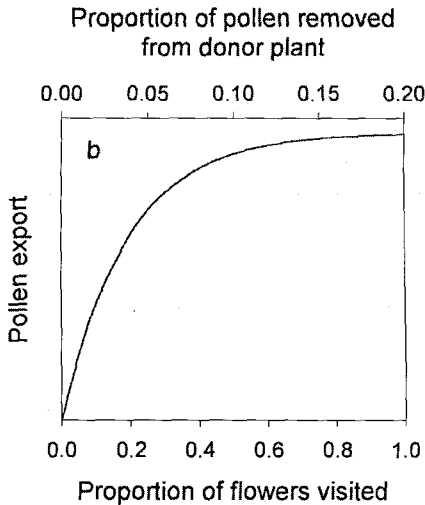
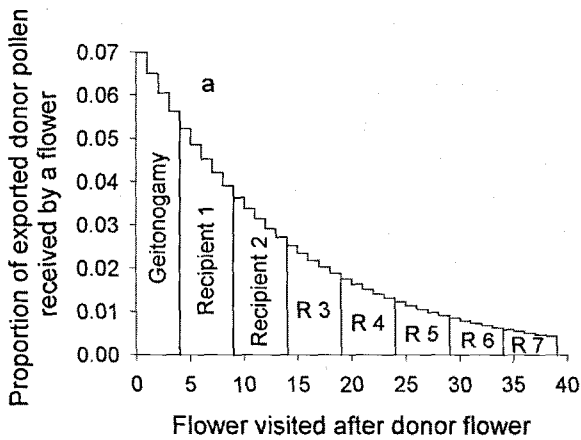


Fig. 15.1. Theoretical features of pollen dispersal by a single pollinator from (a) a single flower and (b) a 50-flowered plant (see Harder & Barrett 1996). Panel (a) considers the pollination fates of pollen removed from the first of five flowers (the donor flower) visited by a pollinator on a focal plant ($d_i = r\rho[1 - \rho]^{i-1}$, where d_i is the proportion of donor pollen received by recipient flower i , r is the proportion of available pollen removed from each flower, and ρ is the proportion of pollen carried by the pollinator that is deposited on the stigma of each flower). Panel (b) illustrates how pollen export from a donor plant (E) to other plants varies with the proportion of flowers that a pollinator visits per inflorescence ($E = r[1 - (1 - \rho)^\nu]/\rho$, where ν is the proportion of the n open flowers visited by the pollinator). For both panels, $r = 0.2$, $\rho = 0.1$, and $n = 50$ flowers.

grooming intensity (and associated pollen loss) varies positively with the amount of pollen removed from a flower (e.g., Harder 1990a), enhanced removal increases subsequent pollen export at a decelerating rate (e.g., Thomson & Thomson 1989). This increased export arises both because each recipient flower receives more donor pollen and because donor pollen reaches more recipient flowers (Harder & Wilson 1998). With layering, total export by a single pollinator initially increases with pollen removal, as each recipient receives more donor pollen. However, greater increases in removal decrease total export, because pollen becomes buried more quickly and so does not reach distant recipients (Harder & Wilson 1998). As we discuss below, the diminishing returns associated with grooming and layering influence the evolution of attractiveness and floral control of pollen removal.

The importance of pollen exchange between flower and pollinator for pollen dispersal by individual pollinators should promote selection for floral features that mediate pollinator–flower interactions to a plant's advantage. Obvious features affecting pollen removal and deposition include corolla size and shape (Murcia 1990; Campbell *et al.* 1996; Kobayashi *et al.* 1999; but see Wilson 1995), the amount and schedule of pollen presentation (Harder & Thomson 1989; Harder & Wilson 1994), anther position (Harder & Barrett 1993), and stigma size, structure and position (e.g., Waser & Price 1984; Murcia 1990; Campbell *et al.* 1994; Conner *et al.* 1995). In addition, pollen exchange often varies with the duration of pollinator visits (Harder 1990b; Murcia 1990; Conner *et al.* 1995; Hurlbert *et al.* 1996; but see Mitchell & Waser 1992), which depends on the amount and quality of food (nectar or pollen) present in a flower (Montgomerie 1984; Harder 1986; Thomson 1986; Martínez del Río & Eguiarte 1987; Harder & Barclay 1994). Because food availability often increases as time elapses since the last pollinator visit (Waser & Mitchell 1990; Kadmon 1992; Williams 1997; Jones *et al.* 1998), flowers exchange more pollen with individual pollinators when they receive infrequent visits than when pollinators visit often (Harder & Thomson 1989; Klinkhamer & de Jong 1993; Harder & Wilson 1994).

Inflorescences

Pollinator behavior on inflorescences

While foraging in the three-dimensional environment of an inflorescence, a pollinator must choose a starting flower, negotiate a route among

visited flowers, and determine when to leave the plant. These decisions affect foraging benefits and costs by determining the number of flowers visited and the time and energy expended on flight. As we discuss in the next section, these decisions also establish the extent of between-flower self-pollination (geitonogamy) and pollen export to other plants.

Many pollinators visiting vertical spikes or racemes invariably start foraging on either lower (bees, wasps, and hawkmoths: e.g., Waddington & Heinrich 1979; Corbet *et al.* 1981; Dreisig 1985; Rasheed & Harder 1997*b*) or upper flowers (flies: Arista *et al.* 1999), thereby predetermining their subsequent movement direction within the inflorescence. For bumble bees, the proclivity to move upward apparently involves a functional constraint, as it persists on inverted inflorescences (Heinrich 1979) or when resources per flower increase or decrease along the inflorescence (Waddington & Heinrich 1979; Corbet *et al.* 1981). Given this constraint, bees respond to resource gradients in vertical inflorescences by altering their starting and leaving positions in ways that enhance their foraging economy (Pyke 1979; Waddington & Heinrich 1979; Rasheed & Harder 1997*b*). By generally moving upward, bumble bees seldom revisit flowers on vertical inflorescences (Pyke 1979; Galen & Plowright 1985). In contrast to insects, hummingbirds move less stereotypically on vertical inflorescences, starting on bottom or top flowers with roughly equal frequency (Wolf & Hainsworth 1986; Healy & Hurly, this volume).

Inflorescences with more three-dimensional structure than a raceme seem to complicate pollinator foraging. The only study to examine this effect (Hainsworth *et al.* 1983) compared the responses of hummingbirds to vertical, two-dimensional inflorescences and hemispheric, three-dimensional inflorescences. On three-dimensional inflorescences, birds probed fewer flowers, with proportionately fewer revisits than when they visited vertical inflorescences. In addition, flights between flowers lasted longer on hemispheric than on vertical inflorescences, even though the flowers were closer together. Hence, the spatial arrangement of surrounding flowers altered the cost of moving between two flowers separated by a specific distance. If this outcome applies more generally, different inflorescence architectures likely establish unique foraging environments for pollinators, and consequently influence pollen transfer within and between plants.

The effect of inflorescence architecture on pollinator behavior depends partly on whether pollinators modify foraging conditions predictably for subsequent visitors by depleting resources. On vertical inflorescences, the

upward movement of bumble bees creates a positive correlation in nectar standing crop among flowers on the same inflorescence (Waddington 1931; Dreisig 1989), so the state of one flower provides information about that of higher flowers. In this environment, a bumble bee invariably continues feeding on its current inflorescence after visiting a rewarding flower, whereas it typically switches to another inflorescence after encountering a single empty flower (Dreisig 1989). In contrast, on the head-like inflorescences, such as *Monarda fistulosa*, bumble bees generally do not leave an inflorescence until encountering several empty flowers (Cresswell 1990). Presumably, this reduced responsiveness reflects the less stereotyped movement of bees on these less ordered inflorescences, thereby limiting correlation in reward availability among flowers (also see Kadmon & Shmida 1992; but see Wolf & Hainsworth 1986). The contrast between these responses indicates that the role of inflorescence architecture in modifying the economics of pollinator foraging (and pollen dispersal) extends beyond the effects of floral display on the actions of individual pollinators to include indirect interactions between all pollinators attracted to an inflorescence.

Geitonogamy and outcross siring success

The presence of multiple flowers permits pollen transport between a plant's own flowers (reviewed by Harder & Barrett 1996; Snow *et al.* 1996; also see Brunet & Eckert 1998; Rademaker & de Jong 1998). In general, geitonogamy increases as a pollinator visits more flowers on a plant. For example, consider the destinations of pollen removed from the first of five flowers visited by a pollinator on a plant (Fig. 15.1a). Geitonogamous pollen transfer from this flower occurs during the pollinator's next four flower visits. If, instead, the pollinator visited eight additional flowers on the same plant, geitonogamy would claim a larger fraction of the total pollen dispersed from the donor flower and the plant as a whole. Because pollinators tend to visit more flowers on larger inflorescences (reviewed by Ohashi & Yahara, this volume), geitonogamy generally increases with display size (reviewed by Harder & Barrett 1996; Snow *et al.* 1996).

In addition to increasing the number of matings susceptible to inbreeding depression, geitonogamy reduces the pollen available for dispersal to other plants (pollen discounting: Kohn & Barrett 1994; Harder & Barrett 1995; Emms *et al.* 1997; Harder *et al.* 2000). Lloyd (1992) proposed that geitonogamy always diminishes outcrossing opportunities when

pollen transport between flowers on the same plant involves the same processes as transport between plants. Because pollen dispersal between a donor and recipient flower varies non-linearly with the number of flower visits that separate them, each additional flower that a pollinator visits adds a progressively smaller increment to total pollen export (see Fig. 15.1b) (Harder & Barrett 1996; Emms *et al.* 1997; Rademaker & de Jong 1998).

The significant mating cost of pollen discounting probably favors inflorescence designs that restrict geitonogamy, including limits on the number of flowers displayed simultaneously, segregation of the sex roles among flowers within inflorescences, and heterostyly (Kohn & Barrett 1994; Harder & Barrett 1995; Harder *et al.* 2000). However, the benefits of specific anti-geitonogamy mechanisms depend on pollinator characteristics. For example, presentation of male flowers above female flowers limits pollen discounting for vertical inflorescences when bees move upward (Harder *et al.* 2000), but would aggravate discounting if pollinators move downward, and would have little effect if pollinators move unpredictably among flowers within inflorescences. Hence, plant species pollinated predominately by animals with different movement patterns should exhibit different patterns of sexual segregation.

Attraction

Many features that distinguish animal-pollinated species from abiotically pollinated species serve the signaling and reward functions that govern a plant's attractiveness to pollinators, including nectar and pollen availability, a showy perianth, and fragrance (reviewed by Mitchell 1993). Attractiveness generally increases with the number of flowers displayed simultaneously (reviewed by Ohashi & Yahara, this volume), and so depends on the aggregate signal perceived by pollinators and their expected foraging returns from a plant's entire floral display (e.g., Weiss 1991). Consequently, the signals and rewards of individual flowers must be considered in the context of their collective contributions to a plant's overall reproductive success.

Given the expense of attraction (reviewed by Morgan 1992), the benefits must be significant. Obviously, a plant must attract enough pollinators to engage much of its pollen in dispersal and to bring in enough pollen to fertilize most of its ovules. Furthermore, participation of many individual animals in pollination increases a plant's mate diversity when different pollinators follow different foraging paths. A less obvious, but

significant, benefit of attracting many pollinators arises because of the diminishing returns associated with increased pollen removal by individual pollinators which accompany pollinator grooming, pollen layering, and geitonogamous pollen discounting. Because of diminishing returns, a pollinator that removes half of a plant's pollen will export more than half as much as another pollinator that removes it all (see Fig. 15.1b). Consequently, plants enhance their pollen export by restricting pollen removal by individual pollinators and involving many pollinators in dispersal (Harder & Thomson 1989; Iwasa *et al.* 1995). Indeed, optimal restriction of pollen removal could increase siring success by more than an order of magnitude when pollinators are abundant, although time-dependent processes, such as loss of pollen viability and competition among male gametophytes for access to ovules, counteract the benefits of restricted removal (Harder & Wilson 1994).

To appreciate the benefits of restricting pollen removal, consider the relation of total pollen export to the proportion of a plant's flowers visited by each pollinator (see Iwasa *et al.* 1995 for mathematical details). Because of the diminishing returns caused by geitonogamous pollen discounting (see Fig. 15.1b), two pollinators that each visited half of a plant's flowers would export more pollen overall than a single pollinator that visited all the flowers, *even though the number of visits per flower is identical*. Attraction of many pollinators further enhances pollen export, as long as each pollinator visits only a fraction of a plant's open flowers, thereby limiting pollen discounting (see Fig. 15.2). However, if pollinators visit too few flowers, pollen can remain in anthers (pollen-removal failure), thereby reducing the plant's total pollen export. Hence, as the solid curve in Fig. 15.2 illustrates, maximization of pollen export occurs when the proportion of flowers visited by each pollinator balances the risk of pollen-removal failure against the mating cost of geitonogamous pollen discounting. The appropriate balance depends on the number of pollinators attracted. Deviation from this optimum reduces total pollen export, particularly when many pollinators visit. However, total pollen export declines asymmetrically on either side of the optimum, so that plants lose less from erring towards too much pollen discounting than from having pollen left in anthers (Fig. 15.2).

Given that enhanced attractiveness increases pollen export only if each pollinator removes a limited amount of pollen, how do plants restrict pollen removal? Two types of mechanisms serve this purpose: *packaging*

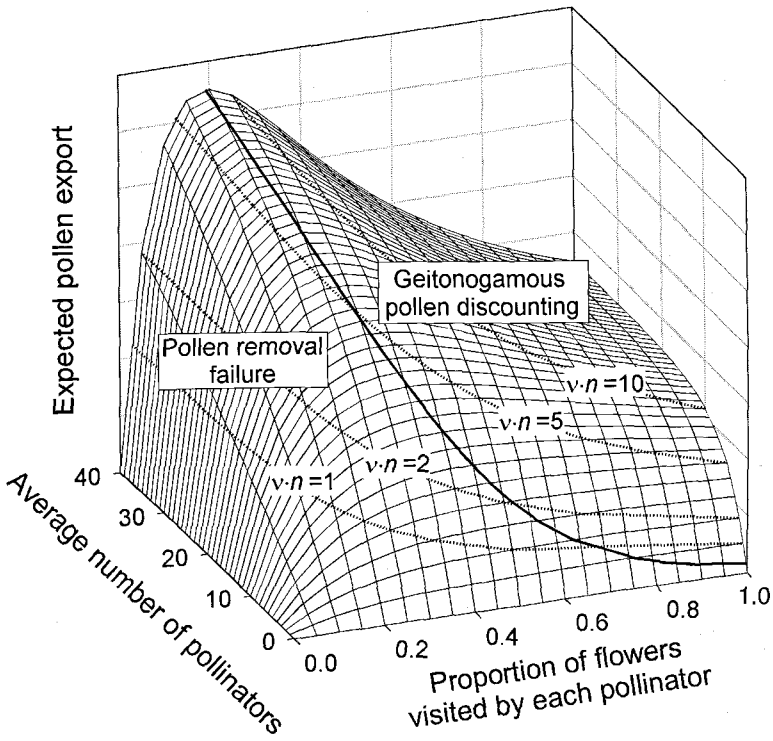


Fig. 15.2. Relation of expected pollen export by all pollinators to average pollinator attraction and the proportion of available flowers visited by each pollinator (based on Eq. 1 in Iwasa *et al.* 1995). The bold solid line depicts the proportion of flowers visited that maximizes expected pollen export for a specific average pollinator availability. Depression of pollen export around this optimum results from pollen-removal failure or geitonogamous pollen discounting, as indicated. The dashed lines illustrate expected pollen export for fixed expected intensities of visits per flower (m). This example involves the same parameter values as Fig. 15.1.

mechanisms control the amount of pollen exposed at one time, whereas *dispensing mechanisms* limit the amount of exposed pollen removed by each pollinator (Harder & Thomson 1989). Packaging mechanisms can be implemented in individual flowers through staggered anther dehiscence, or on the entire plant through staggered opening of flowers. These mechanisms enable strict management of pollen removal because they are completely under a plant's control. In contrast, many dispensing mechanisms adjust pollen removal to a plant's prevailing frequency of pollinator visits

(see Harder & Wilson 1994; Harder & Barclay 1994). Floral mechanisms that serve as dispensing mechanisms include anther position (Harder & Barrett 1993), poricidal anthers (Harder & Barclay 1994; King & Buchmann 1996), secondary pollen presentation (Yeo 1993; Harder & Wilson 1994), anther tripping (Armstrong 1992; Lebuhn & Anderson 1994), and nectar production.

Nectar production provides a unique means of dispensing pollen, because it allows plants to counteract diminishing returns on pollen removal from both individual flowers and inflorescences. Nectar volume influences pollen removal by positively affecting the duration of visits to individual flowers and the number of flowers visited per inflorescence (see above). Because nectar generally accumulates steadily (Búrquez & Corbet 1991), individual pollinators remove less pollen from individual flowers (Jones *et al.* 1998) and visit fewer flowers per inflorescence (Kadmon & Shmida 1992; Hodges 1995) when pollinators are abundant and visits occur frequently. Therefore, the combination of nectar production rate and visit frequency enables restricted pollen removal in a manner that responds to pollinator availability.

In seeming contradiction to this proposal, the rate of nectar production varies considerably among flowers within inflorescences, with some flowers producing little nectar (Feinsinger 1978; Brink 1982; Marden 1984; Gilbert *et al.* 1991). Bell (1986) proposed that empty flowers allowed plants to save some of the expense of nectar production without forfeiting much pollinator service. However, nectar may not be expensive for many plants (reviewed by Harder & Barrett 1992), so that empty flowers may do little to reduce the cost of attraction. Instead, we propose that by maintaining a fraction of flowers that produce little nectar, plants encourage pollinators to leave inflorescences after visiting only a fraction of their open flowers, thereby restricting pollen removal per pollinator and enhancing the aggregate pollen dispersal provided by all pollinators that visit. According to this hypothesis, empty flowers should be most common in species pollinated by abundant pollinators, because restricted removal is most beneficial when pollinators visit frequently.

The preceding discussion of attraction focused on the benefits for male success, rather than female success, through pollen receipt. We adopted this emphasis because the needs of pollen receipt are often realized with fewer pollinator visits than are those of pollen dispersal (e.g., Young & Stanton 1990; Mitchell & Waser 1992; Aizen & Basilio 1998; Bell & Cresswell 1998). This asymmetry arises from the dissimilarity in mating

opportunities through female and male roles. The opportunities for paternal success depend on the number of available ovules in the population as a whole. As a result, outcross siring success increases continuously with a plant's relative contribution of pollen to stigmas. In contrast, each pistil contains a limited number of ovules, so that female outcross success levels off as stigmas receive an increasing share of exported pollen (e.g., Snow 1982; Shore & Barrett 1984; Galen 1992). Indeed, receipt of too much pollen can cause interference between pollen tubes and reduce seed production (reviewed by Young & Young 1992). Because of this asymmetry, the considerable effort expended on attraction by many animal-pollinated plants seems to benefit male success more than female success, even though pollen export must equal pollen import at the population level.

We conclude by emphasizing two essential features of the selection of floral design and display. The first feature arises from recognition that floral and inflorescence characteristics create the environment within which pollinators tend to maximize a specific foraging currency. Because of this role, plant evolution could improve foraging benefits or alleviate costs; however, it will do so only to the extent that such changes promote plant mating (e.g., Harder & Cruzan 1990; Harder & Barclay 1994). Therefore, the evolutionary relevance of specific floral or inflorescence traits must extend beyond their impact on pollinator behavior to realized mating outcomes. The second feature deserving emphasis is that, despite the key role of individual flowers in controlling pollen exchange with pollinators, mating fundamentally involves entire plants. For example, contrary to the expectation that a plant's pollen export increases monotonically with the number of pollinator visits received by each flower (e.g., Harder & Thomson 1989; Harder & Wilson 1994), increasing visits *per flower* with no change in the average number of visits *per plant* eventually reduces export (Fig. 15.2). Because of such non-monotonic effects, selection of floral traits will often optimize pollination of individual flowers to maximize a plant's mating success.

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