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1

Pollen Presentation and Viability Schedules in Animal-Pollinated Plants: Consequences for Reproductive Success

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Introduction: Pollen Presentation Schedules as an Object of Study

Our investigation begins with an observation so commonplace that the reasons for it have scarcely been sought: few plants produce only a single, big anther. In particular, the deployment of pollen accross many anthers and many flowers frequently results in a characteristic temporal schedule of pollen presentation to pollinators. Such schedules, we contend, are an important, but comparatively neglected, component of the floral phenotype.

Percival (1955) pioneered the study of pollen presentation schedules, but her survey of the British flora remained an isolated example for some years. Her work primarily concerned the food value of the plants to pollinators and, therefore, the food choices of the animals. She did point out that gradual presentation was very common. More recent interest in pollen presentation patterns has concentrated on the reproductive success of plants, especially on "male" success through pollen donation. Thomson and Barrett (1981) showed that in *Aralia hispida*, the timing of male-flower anthesis could substantially affect the plant's functional gender (i.e., the relative proportions of its genes that are passed on through pollen and ovules: Lloyd and Bawa, 1984). They argued that selection on male function should favor prolonged pollen presentation, because that would secure more mating opportunities (see also Thomson et al., 1989). Brantjes (1983) invoked weather-induced loss of viability as another selective agent with a similar effect.

Lloyd and Yates (1982; Lloyd, 1984) proposed a more general reason for temporal staggering of presentation: that the mechanics of pollen transfer would often result in a higher proportion of grains being delivered to stigmas if those grains were removed by numerous pollinators rather than by one or a few. Using empirical data on removal and deposition of *Er-*

ythronium spp. pollen by bumble bees, Harder and Thomson (1989) modeled the effects of various pollen presentation patterns on successful donation. This analysis confirmed the Lloyd–Yates conjecture for a generous region of the parameter space examined. Specifically, there will be an optimal presentation schedule for any expected pollinator visitation rate. Infrequent visits favor simultaneous presentation of all pollen, to avoid the pollen wastage entailed by presenting pollen after the last visit. With more frequent visits, however, plants can donate severalfold more of their grains to other stigmas if they package or dispense their pollen so that all visitors encounter some pollen.

The optimal presentation schedules of the Harder–Thomson models are based on a number of simplifying assumptions, including (1) all the grains that reach stigmas are of equal value for male reproductive success, and (2) all pollinator visits are equivalent. Here, we use simulation models to investigate the consequences of realistically relaxing these assumptions. First, we consider the loss of pollen viability that is known to occur in many plants following exposure of the grains. Some pollen will be dead on arrival. Second, we model the effects of different pollinators with different removal and delivery characteristics.

To illustrate the importance of pollen viability schedules, we first address a paradox arising from our observations of *E. grandiflorum*: although this plant provided most of the parameters for the Harder–Thomson model, it appears to contradict that model's principal conclusion. Specifically, casual observations suggest a very *low* visitation rate coupled with *gradual* pollen presentation. Here, we present data on pollen presentation and viability schedules, and on visitation rates, and demonstrate that adding pollen viability constraints to the model can resolve the contradiction.

We then use the new model to ask how presentation and viability schedules affect pollen donation when the suite of pollinators includes different species with different pollen transfer characteristics. Numerous studies have compared the pollination services provided by different flower-visiting animals (e.g., Primack and Silander, 1975; Motten et al., 1981; Tepedino, 1981; Herrera, 1987), but most of these have treated single visits. Only a few have treated multiple visits by individuals of one species or combinations of more than one species (Young, 1988; Young and Stanton, 1990a). Almost none has explicitly considered how temporal patterns of pollen presentation by the plant interact with particular temporal sequences of visits by various pollinators (Tepedino, 1981). Our "pollen depletion" model emphasizes that pollen removed by one visitor is no longer available to be picked up by subsequent visitors, and this essential fact generates some complex consequences for the plants when the pollinators differ in the amount of pollen they subsequently deposit. The value of a particular pollinator to a plant may depend very much on the other pollinators that are available, as well as on the presentation and viability schedule.

Methods

Pollen Presentation Schedules

In May–June 1990, we observed the timing of anthesis and the progress of anther dehiscence in inflorescences of *Erythronium grandiflorum* Pursh (Liliaceae), growing in large, dense stands in subalpine meadows at Irwin, Colorado (39°30′N, 107°6′W, 3275 m elevation). Flowering individuals produce only a few flowers at most; single-flowered plants ("singles") are most abundant, although in certain local areas "doubles" may be as common. Three- and four-flowered plants ("triples" and "quads") are uncommon. Each pendant flower bears six stamens. The anthers are long and thin, typically ca. 1.5 mm in width and 10–25 mm long. Anthers dehisce by "unzipping": a suture opens at the distal end, and the split gradually extends to the proximal end as the thecae turn inside out, exposing the pollen. The amount of pollen contained in an anther can be closely estimated by simply measuring its length (Harder et al., 1985; Thomson and Thomson, 1989). Stigmatic receptivity begins about when dehiscence begins, and extends approximately 1 day after dehiscence is complete, depending on weather and pollination status.

We located, in bud, 16 plants in each flower–number category, one through four. As each flower opened, we marked it and also individually marked the undehisced stamens with dots of ink on the filaments. We measured the length of the undehisced stamens with digital calipers reading to 0.01 mm. Then, at 2-hr intervals during daylight, and 4- or 6-hr intervals during the night, we repeatedly measured the *undehisced* portion of each anther. Observations continued until all anthers of all flowers were completely dehisced. Unfortunately, a number of these plants were lost to herbivores before the completion of anthesis, and many sequences were interrupted by rain.

To consider how pollen presentation schedules might change with an increased number of flowers, we calculated two summary indices for each of the 24 curves we obtained during fair weather. *Duration* is simply the length of time from first dehiscence until all pollen has been exposed. *Evenness* is a measure how evenly pollen is presented over time: the observed presentation curve is broken into hour-long segments, the proportion of grains newly presented (P_i) in each segment i is estimated by linear interpolation between the sequential observations, and the evenness index is calculated as $1/\Sigma(p_i^2)$ (Krebs, 1989).

Pollinator Visitation Rates

Although *E. grandiflorum* flowers are also visited by hummingbirds and small bees, most pollination is effected by large *Bombus* queens (Thomson, 1986). The activity of these insects—and, hence, the visitation rate received by flowers—varies greatly with the weather and with the season. We have noted in several seasons, for example, that the earliest flowers precede the emergence of most of the queens and thus are virtually unattended (Thomson, 1982; personal observation; D. Taneyhill, personal observation). We have not systematically studied variation in visitation rate. For the models in this paper, we required only a rough estimate of visitation under favorable circumstances.

In June 1990, during a sunny period about two-thirds of the way through the flowering season of *E. grandiflorum*, we marked 30 singles with green surveyor's stake flags. These plants were widely spread across ca. 1 ha of the population. All were recently opened, with fewer than three anthers dehisced; all had clean stigmas on inspection by hand lens. We harvested the styles 24 hr after the initial inspection, being careful to prevent contamination. Each stigma was examined microscopically and classified as "unvisited," "possibly visited," or "definitely visited." "Unvisited" stigmas were free of pollen. "Definitely visited" stigmas bore loads of 400 or more grains, deposited in patterns uncharacteristic of autogamous deposition (i.e., in the central cleft of the tripartite stigma and on the downward-facing portions of the papillose stigma lobes). "Possibly visited" flowers had numerous (often ca. 100) grains, but these were typically on the upward-facing and peripheral portions of the lobes. Pollen could have been deposited in these areas without an insect visit, although a visit by a "side-working" bee (Thomson, 1986) could also produce such a pattern. Although subjective, these judgments were informed by considerable experience in observing and counting stigmatic loads produced by *Bombus* visits.

We estimated the visitation rate (as visits flower^{-1} day^{-1}) from the fraction of flowers visited, by assuming a Poisson process (i.e., the fraction of unvisited flowers equals e^{-m}, where m is the mean number of visits per flower). Because the flowers were widely spaced, we expect that the independence assumption of the Poisson was adequately met. To circumvent the ambiguity caused by the "possibly visited" category, we calculated the visitation rate twice, once with these flowers counted as visited and once with them counted as unvisited. The resulting two estimates delimit a range that probably contains the true value.

Viability of Pollen

In a small experiment in June 1989, M. B. Cruzan and N. O'Connor used the fluorochromatic reaction (FCR) test (Heslop-Harrison et al., 1984; Shivanna and Johri, 1985) to determine how long *E. grandiflorum* pollen grains remained viable after exposure, on the dehisced anther, under field conditions. Freshly cut flowers were kept in vases. Initially, a sample of ca. 200 grains was taken from the splitting cleft of one dehiscing anther from each flower; these were the freshest grains possible. At intervals, further samples of grains were removed from the same area of the anther. Because the cleft moves as the anther unzips and shrinks from desiccation, there is no reference point to assure that one is resampling from precisely the same spot, but this was attempted.

Each sample of grains was treated with a 10% sucrose solution to which fluorescein diacetate in acetone had been added dropwise until the mixture became cloudy. After culturing for a few minutes under a cover slip, at least 100 grains were examined under UV. Brightly fluorescing grains were scored as viable.

Pollen-Depletion Models

We wrote FORTRAN programs (available on request) to investigate the effects of pollen presentation schedules, viability schedules, and mixed pollinator faunas. These simulation models track pollen movement from a plant over a period of anthesis divided into 100 (200 in some runs) equal intervals.

Each model starts with a "pollen presentation curve," or a plot of cumulative number of pollen grains made available to pollinators through the 100 time intervals. During each interval, whether a pollinator visits or not is determined by a random number between 0 and 1, which is compared to a chosen probability. For example, if the probability is 0.1 per interval, 10 randomly spaced visits are expected during anthesis. For simplicity, only one visit is allowed per interval. During a visit, the pollinator moves some of the available pollen from the anthers, leaving the rest behind. Of the removed pollen, some is subsequently deposited on recipient stigmas. Removal and deposition are governed by deterministic functions whose parameters are simplified versions of those measured empirically by Thomson and Thomson (1989) and Harder and Thomson (1989) for the *Erythronium*–*Bombus* system. When the next pollinator comes, the pollen presented comprises the residuum left after the first visit, plus any newly presented pollen, as determined from the presentation curve. The total number of grains deposited on other flowers by all visitors is calculated from the (pollinator-specific) deposition function. This measure of pollen donation can serve as an index of expected plant reproductive success, in situations where pollen receipt does not limit female function. We ignore self-deposition in estimating male success because competitive pollinations indicate that self-pollen seldom fertilizes ovules when outcross pollen is also present

(Rigney et al., 1992). All results are based on 500 iterations. Parameter values and other details for specific simulations are given below, with the results, for ease of interpretation.

Results

Pollen Presentation

Pollen presentation is far from simultaneous in a plant of *E. grandiflorum* (Figs. 1.1 and 1.2). The six anthers are grouped into two whorls, and the outer whorl of three opens before the inner whorl. Often, dehiscence is complete in the outer whorl before it has begun in the inner; less commonly, there is some overlap. Within a whorl, the three anthers often show staggered openings.

Anthers unzip most quickly in warm, dry weather; dehiscence continues overnight, but at a slower pace, contributing a somewhat steplike character to the cumulative presentation curves (Figs. 1.1 and 1.2). Partial synchronization of anthers within whorls also contributes a step-like component. The gradual overnight presentation of pollen in the absence of visitors will presumably result in an accumulation of grains for the first visit of the morning. Otherwise, cumulative presentation is almost linear during the day.

Overcast weather with high relative humidity greatly slows anther dehiscence. If enough rain falls to wet the anthers, the unzipping process can actually be reversed, as the rehydrated anthers appear to close. Clearly, such reversals make it difficult to estimate cumulative pollen production. There were two rainy periods during our study, and, for simplicity, we have removed from the data set all of the plants that were caught in mid-presentation by either of these rains. Thus, the data represent dehiscence patterns under better-than-usual conditions.

Adding more flowers to the inflorescence could, in principle, change the duration or the evenness, or both, or neither. Duration would be increased by opening the flowers sequentially, rather than simultaneously; evenness could be affected if different flowers have staggered periods of most rapid presentation, thus averaging out presentation over time. Only a few of the multiple-flowered plants escaped the rainy periods, giving small sample sizes. Nevertheless, Figure 1.3 makes it clear that duration increases with flower number, and hints that evenness is maximized in three-flowered plants. Flowers generally open sequentially in *E. grandiflorum*, often with no overlap. Uppermost flowers are the largest, open first, have the most ovules, and are most likely to set fruit (Thomson, 1989). In triples, the lower two flowers usually follow the same pattern (i.e., the second to open is larger and more likely to set fruit than the third, but occasionally the

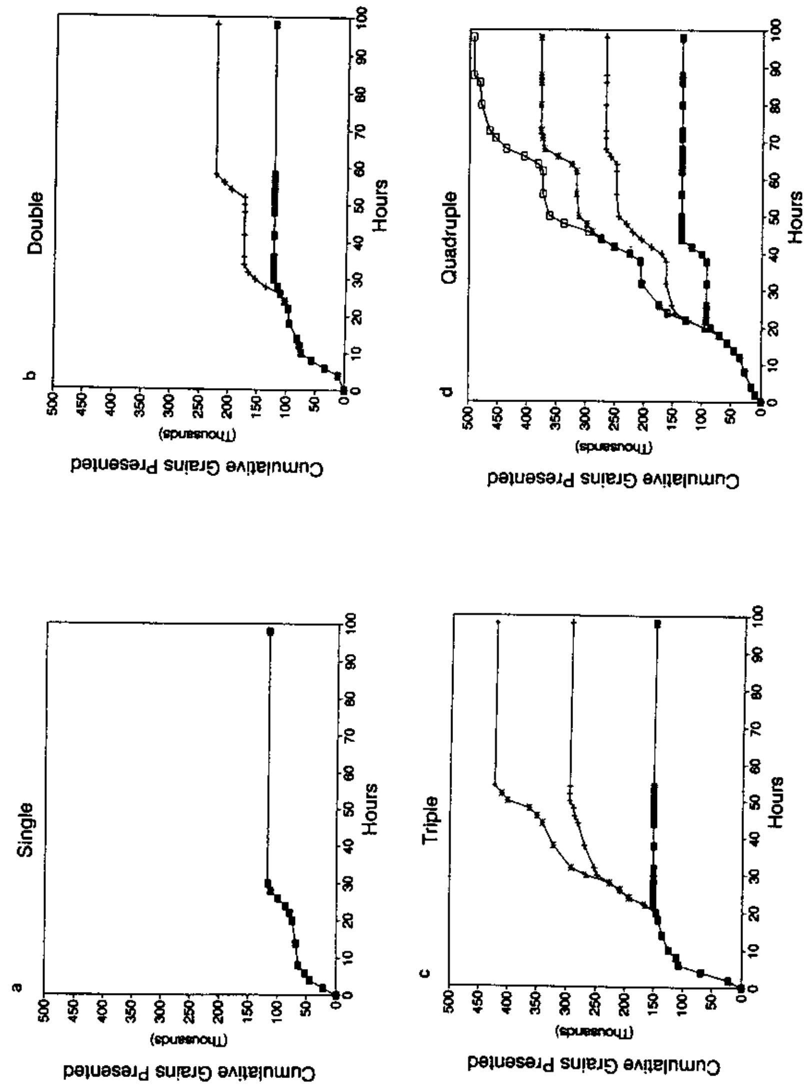

Figure 1.1. Observed pollen presentation curves for typical *Erythronium grandiflorum* plants with different numbers of flowers. (a) A single-flowered plant; (b) a double; (c) a triple; (d) a quadruple. In b–d, the graphs are stacked, so that the lowest line shows the pollen presented by the first flower, the next line shows the total amount

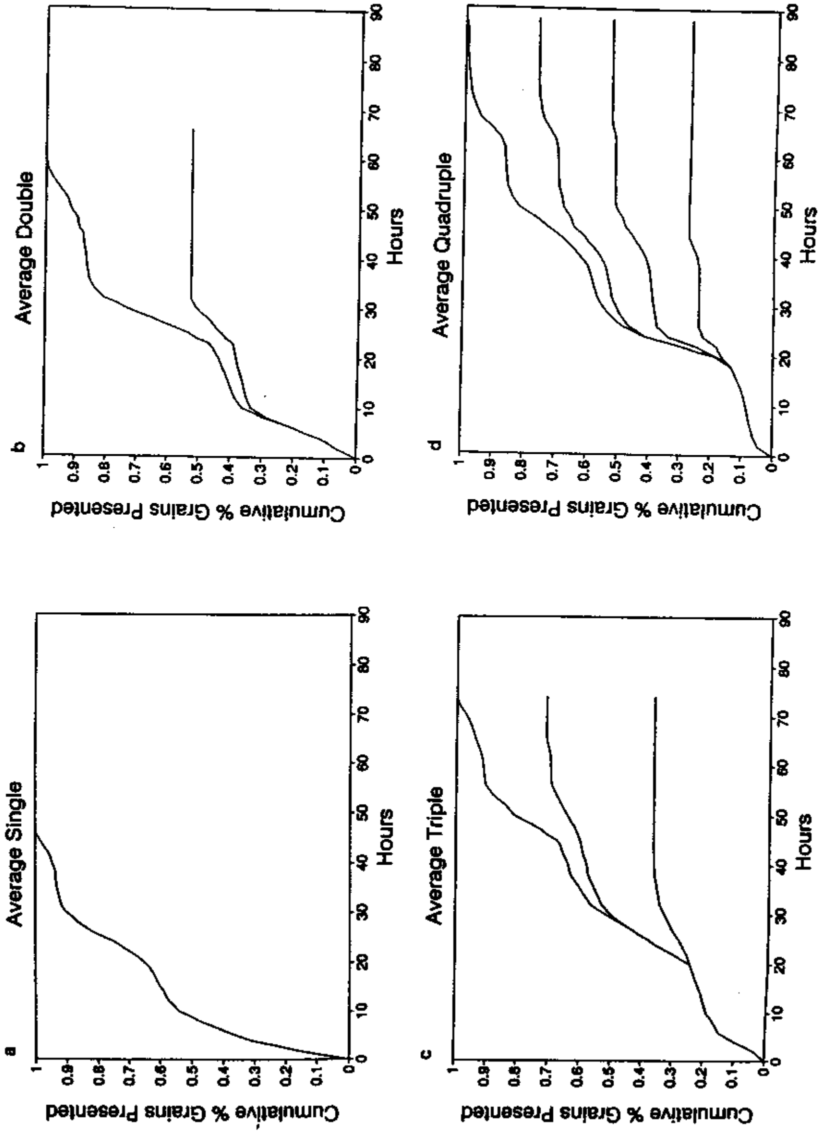

Figure 1.2. Average pollen presentation curves for *Erythronium grandiflorum* plants from different flower–number classes (a–d as in Fig. 1). Averages were computed by first interpolating grain numbers for each flower in a class so that all flowers had a number of grains presented for every hour. Sample sizes are 11, 7, 3, and 3 plants for panel a, b, c, and d, respectively.

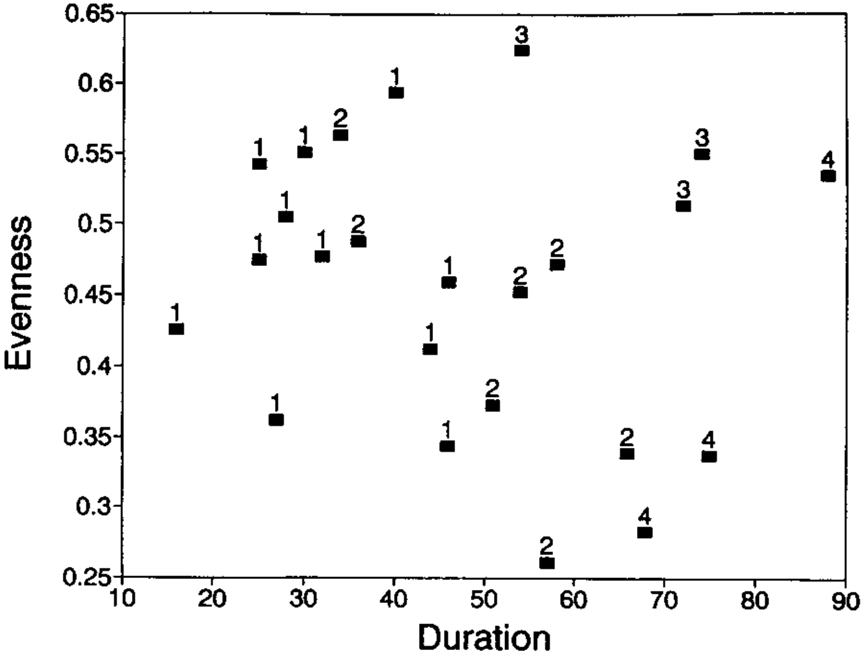

Figure 1.3. Temporal evenness of pollen presentation vs. duration of pollen presentation for *Erythronium grandiflorum* plants from different flower–number classes. Numerals by each point indicate the flower–number class of the plant.

lower two appear as "identical twins," borne at the same point on the scape, of the same size, and undergoing anthesis in parallel). We believe that the probability of such twins increases in quadruple inflorescences, possibly limiting the average evenness obtained by such plants.

Visitation Rate

The fraction of flowers "definitely visited" and "possibly visited" during the 24-hr test period were 0.57 and 0.80, respectively ($n = 30$), leading to minimum and maximum estimates of visitation rate of 0.65 and 0.82 visits flower^{-1} day^{-1}. As these estimates reflect the most favorable weather conditions, realized visitation rates are almost certainly lower, on the order of one visit per flower lifetime. Thomson (1982) reported visitation rates in this same general range at another site, using different methods.

Pollen Viability

FCR scores declined rapidly with time of exposure (Fig. 1.4). Desiccation is the most likely cause of the decline; drying of pollen is known to damage

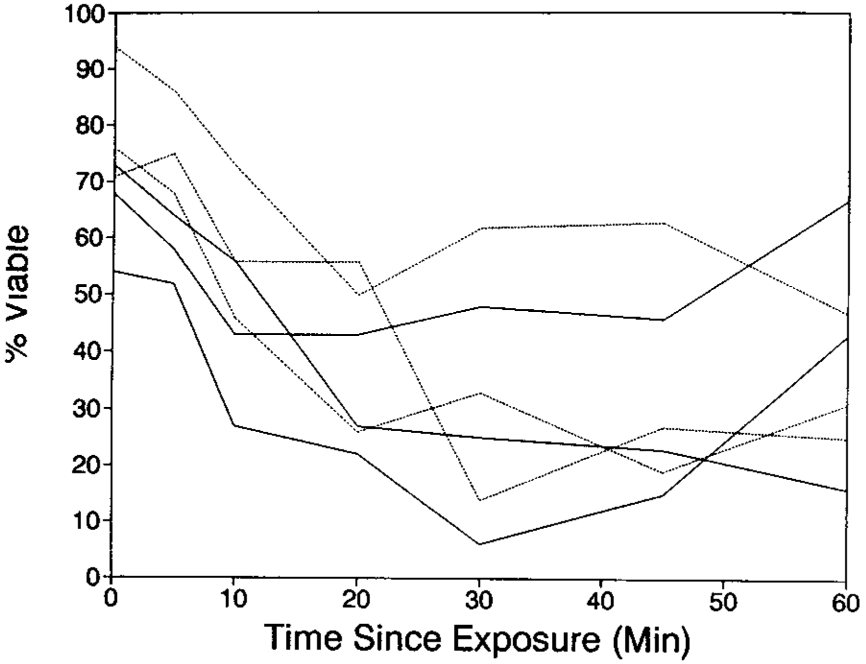

Figure 1.4. Time course of viability loss for *Erythronium grandiflorum* pollen exposed to field conditions for various lengths of time. Each line represents pollen taken from a single anther. The broken lines are data from 7 July 1989, a sunny day; the solid lines are from 8 July, a cloudy day.

membrane function (e.g., Shivanna and Johri, 1985; Hoekstra and van Roekel, 1988), and the FCR procedure assays membrane function (as well as enzyme activity). It is not certain that the nonfluorescing grains are truly dead; exposure to a humid atmosphere might well restore membrane integrity and, with it, pollen function (Shivanna and Johri, 1985; Linskens et al., 1989). Nevertheless, dehydrated grains will probably be slower to germinate on stigmas and thus be less likely to contribute to reproductive success than fresher grains. Additional experiments from 1991 have confirmed the general shape of the pollen survival curve and have suggested that the apparent "resurrections" seen in some curves in Figure 1.4 are probably artifacts due to againg of the fluorescein diacetate solution (Karoly et al., 1992).

Simultaneous vs. Gradual Presentation of Pollen

The data on visitation rate and on pollen presentation raise an apparent paradox. *Erythronium grandiflorum* appears to stagger pollen presentation

nearly as much as its morphology allows, yet the models of Harder and Thomson (1989) suggest that rarely visited plants should *not* stagger presentation. To confirm that the observed presentation phenotype appears maladaptive under the Harder–Thomson assumptions, we modeled a situation in which the expected number of bee visits was either 1.0 or 10.0 during the life of a plant. Each visit removed 70% of the available pollen, and the number of grains subsequently deposited on other stigmas is estimated by the square root of the number of grains removed. These values approximate the mean values found for bumble bee visits by Thomson and Thomson (1989).

In addition to varying visitation rate, we used three different pollen presentation curves: one observed curve, taken from a typical two-flowered plant, and two hypothetical extremes. In one extreme, all grains were presented simultaneously (no staggering); in the other, equal numbers of grains were presented in each interval (complete staggering).

The total amount of pollen donated by the hypothetical plant with simultaneous pollen presentation was *greater* than that of either the observed phenotype or of the completely staggered plant when only a single visit is expected (Fig. 1.5a). The advantages shift more toward the staggered schedules when more visits are expected (Fig. 1.5b), in accordance with the expectation above.

If, however, the model is further modified so that pollen gradually loses viability after it is exposed in the anthers and if only viable grains are counted toward the total donated, the observed phenotype becomes superior to the simultaneous presenter (Fig. 1.5a), even at low visit numbers. The combination of low visitation and short-lived pollen probably best represents the conditions governing *E. grandiflorum* pollination. In these runs, pollen survival was modeled as an exponential decay process, with 10% mortality of the grains in each time interval. Formulating this loss rate in terms of typical *Erythronium* pollen presentation curves yields a pollen half-life of about 3 hr (6 intervals to 50% decay, 100 intervals per approximately 50-hr anthesis period). This is a conservative loss rate, in view of our preliminary data on viability schedules (Fig. 1.4).

Different Types of Pollinators

In this set of simulations, we consider the effects and interactions of three pollinator types that differ in their removal and delivery of pollen. For mnemonic convenience, we name the types "*good*," "*bad*," and "*ugly*," and for brevity we will consider them all to be bees, although they could represent any type of pollinator (Table 1.1). Good bees remove large amounts of pollen and redeposit it in relatively large amounts; their parameters are simplified versions of functions measured for bumble bees on

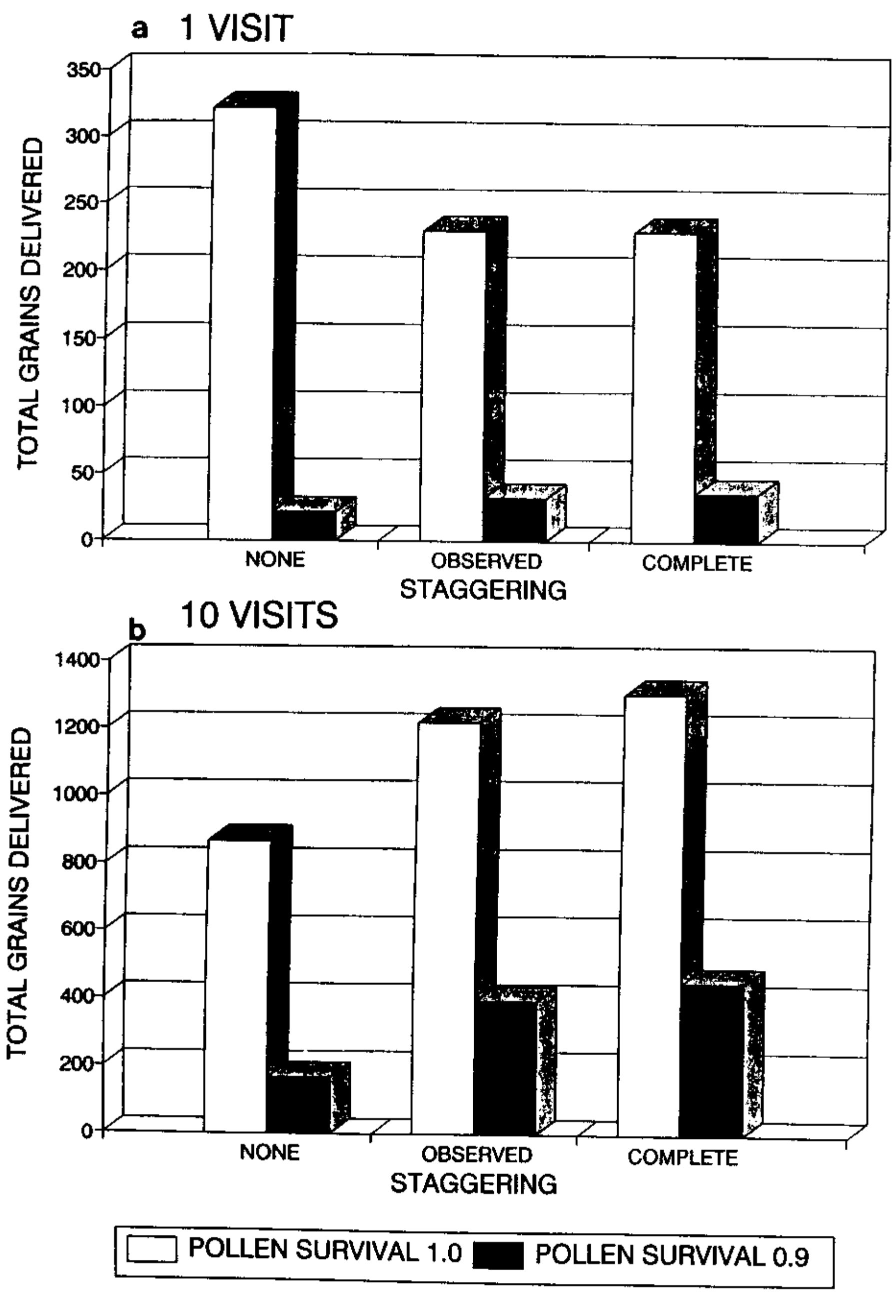

Figure 1.5. Results of simulation model of pollen delivery for three pollen presentation schedules, two viability schedules, and two pollinator visitation rates.

Table 1.1. The Deterministic Pollen Removal and Deposition Functions Used to Model the Three Different Types of Pollinators.[a]

Function	Pollinator type		
	Good	Bad	Ugly
Removal	$R = 0.7P$	$R = 0.2P$	$R = 0.7P$
Deposition	$D = R^{0.5}$	$D = R^{0.4}$	$D = R^{0.4}$

[a] P, number of grains presented in anthers at time of visit; R, number removed by pollinator; D, number of removed grains subsequently deposited on stigmas. The values used for the good pollinator approximate those observed for *Bombus occidentalis* queens on *Erythronium grandiflorum* (Thomson and Thomson, 1989; Harder and Thomson, 1989); the others are judged to be reasonable approximations for hypothetical pollinators that pick up and deposit less pollen.

Erythronium. We view these parameters as representing a situation of reasonable coadaptation of plant and pollinator. The other two categories are hypothetical variants. *Bad* bees remove less of the available pollen and deposit less of what they remove. They have relatively little impact on pollen flow. *Ugly* bees, in contrast, remove pollen as do good bees but deliver what they remove as do bad bees. They move more pollen than bads but also take a larger amount out of circulation. Other variants could be considered, of course, but these are sufficient to produce complex interactions.

A good bee always delivers more pollen than the others, but the relative values of the others to the plant depend on other parameters (Fig. 1.6). When presentation is staggered and pollen is immortal, all three bees deliver pollen as a slightly decelerating function of visit number (Fig. 1.6a). The bad and ugly bees both deliver about one-third as much per visit as good bees. If these long-lived grains are instead presented simultaneously, both good and ugly bees deplete the anthers of pollen fairly quickly, yielding saturating curves of delivery vs. visit number (Fig. 1.6b). Pollen delivery by ugly bees saturates at about 39% of the saturation level for good bees. The bad bees, less effective at removal, do not deplete the anthers so quickly, and their curve continues to rise, crossing that of the uglies at about four visits. Under these conditions, the relative values of bads and uglies as pollinators are not absolute, but depend on the number of visits, with the bad bees becoming more valuable as they are more common.

Having short-lived pollen changes things. With staggered presentation, none of the curves shows satuation over the range shown, and the uglies are almost twice as effective as the bads (Fig. 1.6c). This relatively better performance by the uglies shows how low pollen viability puts a premium on high removal, even if subsequent delivery to stigmas is not very effective. Unremoved grains will soon die in the anthers in any case, so there would

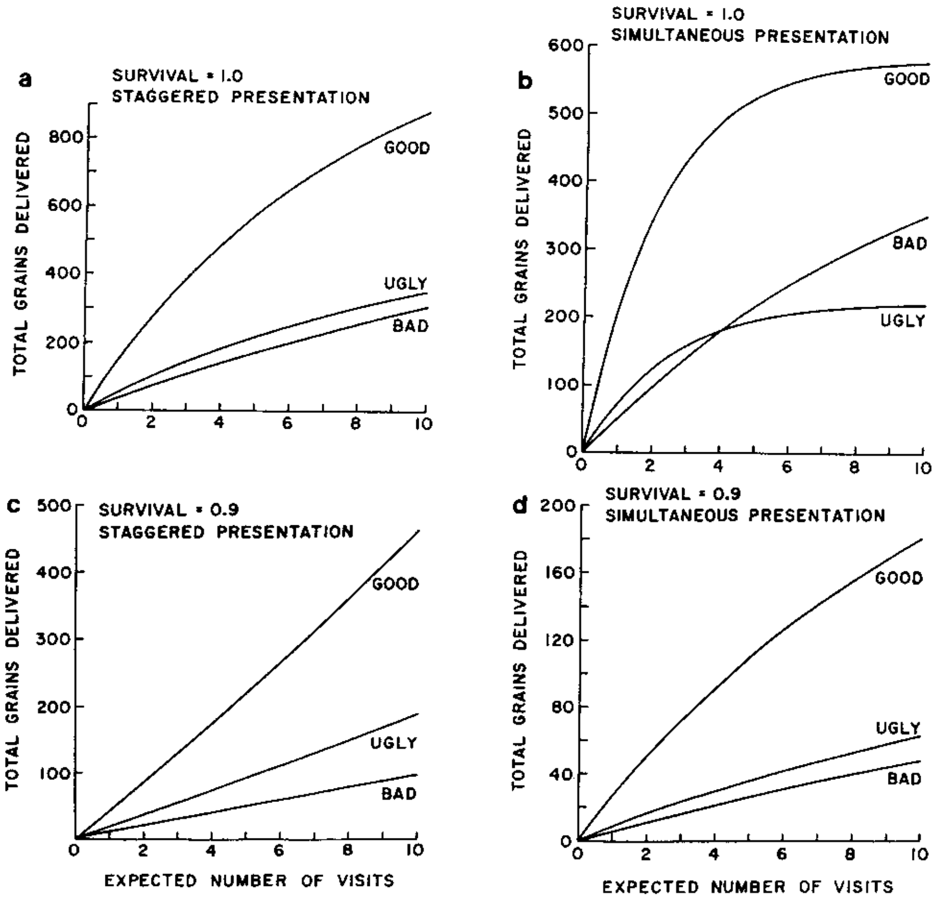

Figure 1.6. Results of simulation model of pollen delivery as a function of expected visit number by three hypothetical pollinator types (see Table 1.1 for the pollinator characteristics) under four combinations of pollen viability and presentation schedules. Note different vertical scales.

be little advantage in their "waiting" for a better pollinator to arrive. The curves do not saturate (1) because staggered production prevents depletion of the anthers and (2) because each of the many small cohorts of grains has a short life and thus needs a visit during that short life to achieve effective dispersal.

When short-lived pollen is presented simultaneously (Fig. 1.6d), the curve shapes are very similar to those for staggered, long-lived pollen (Fig. 1.6a), but total amounts of viable pollen delivered are very different. The agreement in shapes seems fortuitous, as the parameters of the model are so different.

We also explored the consequences of mixed groups of pollinators. In our simulations, we examined mixtures either of goods and bads or of goods and uglies. At each interval of the pollen presentation curve, a random number was chosen to determine, with a certain probability, whether or not a visit would occur. If a visit did occur, a second random draw determined whether the visitor was a good bee or of the other type (bad or ugly, depending on the run). Thus, both the expected total number of visits and the fraction of those visits made by good bees varied stochastically in these runs.

In addition to confirming that pollen delivery is increased by more visits and by a higher proportion of good visits, these simulations reveal some of the complexities and nonlinearities that govern how two different pollinators interact (Fig. 1.7). Some of these parameter combinations are explored in Table 1.2. Under the conditions outlined in Table 1.2, we see that four uglies alone deliver 1.41 times more grains than four bads alone. We might tend to conclude, therefore, that uglies are simply better than bads for plants with the indicated presentation and viability schedules. However, if four good bees are *also* visiting, the values of the bads and uglies reverse. Four uglies *add* only 528 − 492 = 36 grains to the number that would have been delivered by the four good bees alone; four bads *add* 1.92 times that amount. In this situation, the ugly bees live up to their mnemonic; although the ugly bees are more effective than bads when by themselves, they do not combine well with better bees.

If we examine the same comparison with short-lived pollen, bad and ugly reverse again (Table 1.2). Four ugly bees now *add* 1.77 times more grains to the amount delivered by four goods alone than do four bads. Once again, short-lived pollen puts a premium on removal; in this simulation, four ugly bees *add* more grains when in the company of goods than they deliver alone.

The final comparison—long-lived pollen, simultaneously presented–reveals ugly bees at their ugliest (Table 1.2). Here, *adding* four visits by ugly bees to four visits by good bees actually *reduces* total pollen delivery by 21%. Adding bads *increases* delivery by 7%. That adding uglies reduces total delivery is doubly striking: first, the ugly bees are good pollinators when they alone visit. In fact, they are as good as the bads. Second, eight visits, all by effective pollinators, deliver less pollen than four of those visits would alone. The peculiar interaction of the two bees with the presentation and viability schedules turns the less effective pollinator into a functional parasite. Its "crime" is that it removes pollen that, if left behind, would be delivered better by the other visitor.

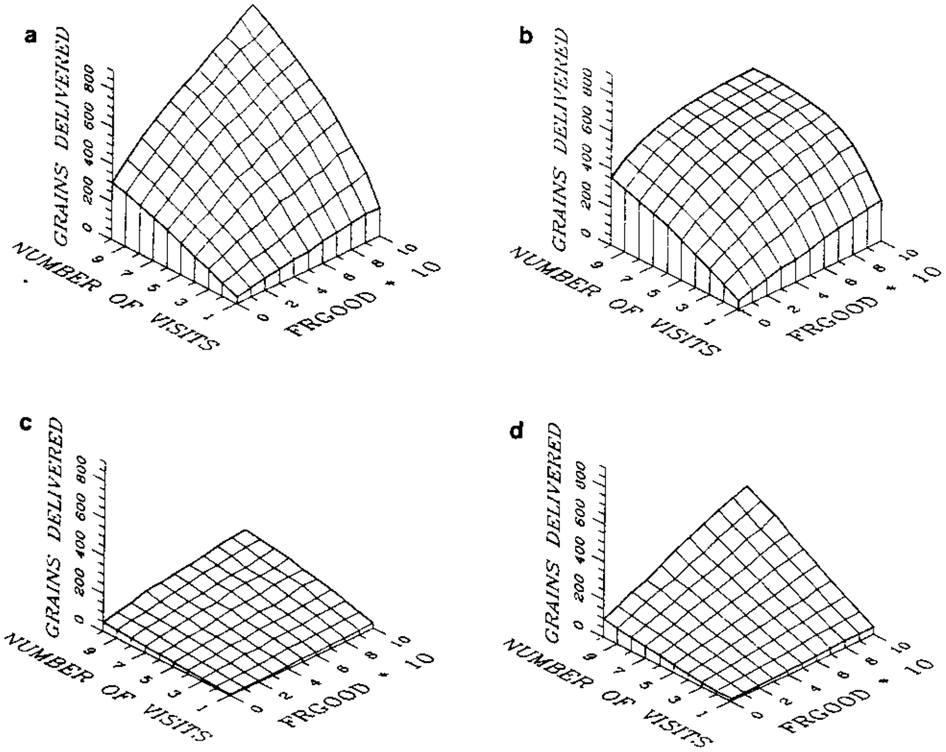

Figure 1.7. Results of simulation models of pollen delivery as a function of the abundances of different hypothetical pollinator types. (a–d) Mixtures of good and bad pollinators; (e–h) mixtures of good and ugly pollinators. The axis labeled "FRGOOD * 10" indicates the expected proportion of visits that are by good pollinators (multiplied by 10 for the convenience of the graphing package used). (a and e) Long-lived grains and staggered presentation; (b and f) long-lived grains and simultaneous presentation; (c and g) short-lived grains and staggered presentation; (d and h) short-lived grains and simultaneous presentation.

Discussion

We began this work with the idea—derived from our measurements of pollen removal and delivery—that pollen presentation schedules should become objects of quantitative study for evolutionary ecologists. We ended by concluding that pollen viability schedules deserve equal attention. To paraphrase George Williams on life history attributes: *schedules*, no less than teeth or chromosomes, evolve. However, measuring these schedules

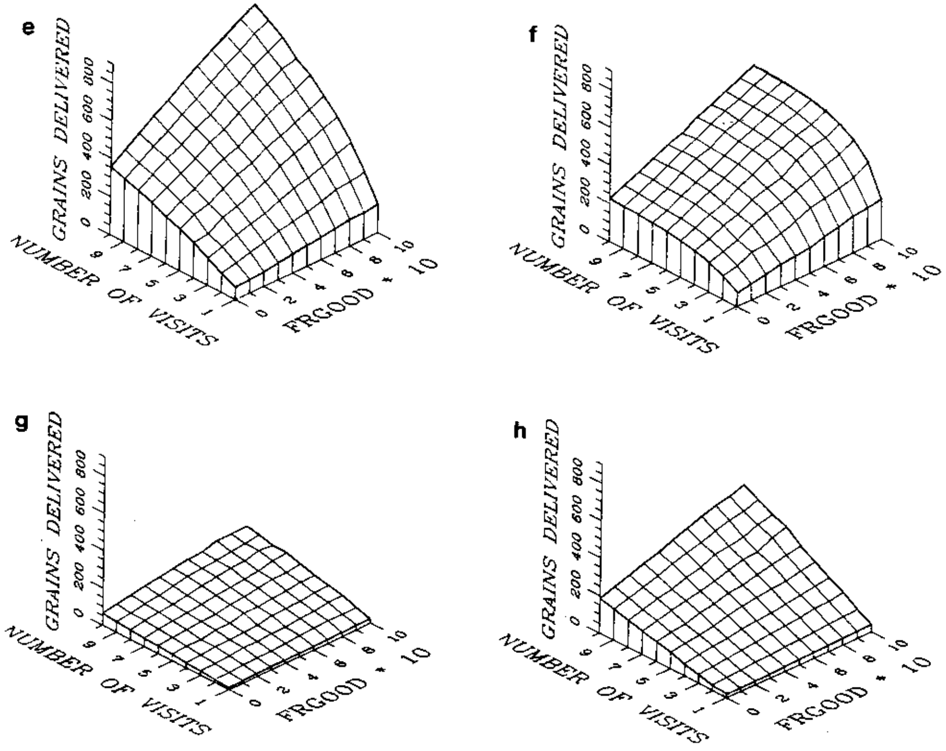

Figure 1.7. (*Continued*)

Table 1.2. Interaction of Different Pollinators for Some Selected Parameter Combinations Extracted from Figure 1.7.[a]

Expected set of visits	Total viable grains delivered Long-stag	Short-stag	Long-simul
4 goods only	492	173	492
4 bads only	133	36	179
4 uglies only	187	67	181
4 goods + 4 bads	561	218	525
4 goods + 4 uglies	528	252	390

[a] Long, long-lived pollen; short, short-lived pollen; stag, staggered presentation; simul, simultaneous presentation.

poses practical difficulties, which we will discuss briefly before taking up more subtle points of interpretation.

Measuring pollen presentation schedules seems straightforward in principle. Although few plants have large, linear, "unzipping" anthers like those that allowed us to follow gradual dehiscence at the individual stamen level in *Erythronium*, such detail may be unnecessary in plants with smaller anthers. But harder problems come in deciding which aspects of the measured presentation curves are relevant. Our analyses included whole curves, measured on a 24-hr basis. Our simulations send in visitors at random times, regardless of day or night. Although suitable for heuristic purposes, such simplifications would compromise any applied study. To do better, however, would require additional details on the diel patterning of pollinator visits, which requires a particularly demanding and tedious variety of field work.

Equally worrisome is the effect of weather. We achieved simplicity by ignoring rainy periods, but this cost us two-thirds of our data. More importantly, natural selection on pollen presentation schedules does not, presumably, ignore rainy periods. Even mild overcasts and temperature fluctuations influence dehiscence; they influence animal pollinators as well. A complete analysis of a real system must tie weather variation to both supply and demand aspects of pollen–pollinator interactions. Furthermore, desiccation (as cited by Brantjes, 1983) is not the only cause of pollen death; grains that stay too long in undehisced anthers due to humid weather may lose viability as well (Linskens et al., 1989), an additional factor to measure and model. We need a more integrative view of weather in floral biology; humidity and temperature will certainly be important driving variables (see Corbet et al., 1979).

A more enjoyably solved challenge of this pollen–demographic approach will lie in establishing more communication between evolutionary ecologists concerned with the fitness consequences of floral phenotypic variation and physiologists, who have developed most of our understanding of the basic processes of dehiscence, viability, and germination. Both groups need to understand each other's literature before some of the most basic questions can be answered satisfactorily. One of the most important of these is: "How should viability be measured?" It is clear that none of the traditional "stainability" methods gives the same information as the FCR test itself, and it is equally clear that the FCR test does not always predict germinability (Shivanna and Johri, 1958). For models like ours, we need to know more about the prospects for *partially* desiccated pollen to sire seeds after landing on a stigma along with fresher grains. Pollen variability tends to be treated as a "+/–" condition, but there may be considerable variation in vigor among the viable grains (Young and Stanton, 1990b). We are beginning such studies on *Erythronium*, using electrophoretic markers to determine the success of stressed pollen in competitive pollinations.

Pollen Removal and Deposition by Different Visitors

Detailed studies of removal and deposition are still rare and mostly recent (e.g., Strickler, 1979; Snow and Roubik, 1987; Wolfe and Barrett, 1989), but seem to be increasing. The advent of electronic particle counters has made pollen counting so quick that new types of study are practical. Because directly estimating a plant's male reproductive success is so difficult, several workers have proposed using the amount of pollen removed from a plant's anthers as an index of male success (e.g., Cruzan et al., 1988; Young and Standon, 1990a; Murcia, 1990). Although these indirect estimates are better than more primitive estimates, such as the number of visits (e.g., Thomson, 1988), pollen removal can be a very poor index of subsequent pollen delivery, especially if pollinator faunas are heterogeneous. "Ugly" pollinators may contribute to high removal rates, even as they decrease successful delivery. Such outcomes are not purely hypothetical; Wilson and Thomson (1991) have demonstrated that pollen-foraging honey bees do play the role of "ugly" pollinators in *Impatiens capensis*, where nectar-feeding bumble bees are the "good" pollinators. Patches dominated by the honey bees show higher removal rates but lower stigmatic deposition. One cannot draw valid inferences from removal data without knowing something about the pollinators.

The necessary information is virtually unavailable in the literature. Few existing studies of the differences among pollinators consider multiple visits (Young, 1988; Young and Stanton, 1990a; Murcia, 1990; and Harder, 1990a provide exceptions) or simultaneously quantify both removal and deposition. Thus, most studies imply that a particular visitor has a fixed pollination value. In contrast, our pollen-depletion models show that the value of any single visit depends greatly on what other visits have previously occurred or will occur in the future.

There are two especially weak links in our model; both concern the removal and delivery functions. First, all our knowledge of removal in *Erythronium* comes from first visits. The models assume that freshly presented pollen and pollen remaining after a visit have identical removal characteristics. In fact, the pollen remaining may have remained precisely because it resisted removal (e.g., it may have been stuck to tapetal tissue or wedged in fissures). This issue—the equivalency of fresh pollen and remaining pollen—is hard to approach experimentally.

Second, we use deterministic functions for removal and deposition, even though these processes are actually highly stochastic. The empirical relationship between pollen removal and subsequent deposition (Thomson and

Thomson, 1989; Harder and Thomson, 1989) shows so much scatter that fitting *any* function through the points is partly an act of faith and needs to be bolstered by other knowledge (e.g., the positive relation between pollen load on the bee and the bee's rate of grooming (Thomson, 1986; Harder, 1990b). We use these data because better data do not exist, and we use deterministic functions to clarify the contrasts between the different pollinator types in a model with heuristic intent. Any attempts to measure significant differences in pollen transfer by different pollinators will require very large sample sizes, due to the highly stochastic nature of anther and stigma contact (P. Wilson, personal communication; see Thomson, 1986).

It will also be important to measure deposition as completely as possible. If deposition is measured only on the first few recipient flowers, for example, a pollinator with very extensive pollen carryover might appear to be "ugly," whereas in fact it might provide superior pollen delivery (M. Stanton, personal communication).

Furthermore, natural selection on floral phenotypes, including scheduling aspects, will also reflect, and will be impeded by, the great stochasticity of pollen transfer. Our models present an unusually "clean" view of the linkage between phenotype and fitness.

Visit Sequence

Our models assume a randomized order of arrival of the two pollinator types. This assumption is crucial; ugly bees, for example, would have no detrimental effects if their visits occurred after the visits of the good bees. In some real situations (e.g., honey bees vs. bumble bees), random arrivals may be an acceptable assumption, but in others [e.g., those involving early-morning or "matinal" bees such as *Peponapis* (squash bees) (Tepedino, 1981)] sequential arrivals of different visitors may be predictable and important. In such cases, pollen depletion by the early visitors may render later visitors completely ineffectual and therefore of no evolutionary importance to the plants. It would be interesting to see whether matinal solitary bees are more likely to show oligolecty than nonmatinal species.

Practical Implications

In numerous agricultural crops, harvests are typically limited by insufficient pollinations (Free, 1979; Robinson et al., 1989). The near-universal "remedy" is to bring in hives of honey bees. Even though honey bees are known, in some cases, to be less effective pollinators than certain wild bees (Parker et al., 1987), there appears to be a common feeling that one can always bring in enough of them to "saturate the system." Our models suggest two caveats. First, honey bees are often very active pollen collectors. Although Free (1970) implies that pollen-foraging bees are likely to be better pollinators than nectar collectors, this is hardly necessary; an efficient pollen collector that often misses the stigma will still be an "ugly" bee. This is true of honey bees on *Impatiens capensis* (Wilson and Thomson, 1991), and it may be true in some agricultural systems. If so, adding honey bees may be ineffective or even harmful. Furthermore, even if there are no negative effects, "saturating the system" may involve pollen *delivery* saturating as a function of visit number as in Figure 1.6B. Under the conditions depicted, one could add an infinite number of ugly bee visits without equaling the pollen delivery provided by only three good ones. It would be worthwhile to know more about bee-specific pollen transfer dynamics before embarking on a managed system of pollination by honey bees or before calculating the cash value of pollination services provided by honey bees (Robinson et al., 1989).

Competition

When we have spoken of adding bees to a system, we have assumed no interaction between pollinators (e.g., we "add" four uglies by comparing pollen transfer by four goods alone to that by four goods plus four uglies). In real systems, competition among pollinators might occur, such that adding new pollinators would entail the loss of some old ones. The surfaces in Figure 1.7 can be used to make simple comparisons of this sort. Generally, competition makes bad pollinators worse, but the effects vary greatly depending on other parameters. Competition effects should also be considered when supplementing (supplanting?) wild bees with managed hives.

Conclusion

The male reproductive success of a plant depends on the amount of pollen it donates to stigmas. In animal-pollinated plants, this amount is influenced by the schedules of pollen presentation, pollen survivorship, and pollinator visits. Although each of these factors acts in a straightforward, comprehensible way when only a single pollinator type is attracted, heterogeneous pollinator faunas produce complicated interactions with the scheduling variables. Consequently, the value of a given pollinator to a plant may vary from positive to negative depending on context. Also, two pollinators may have very different values to plants that are identical in all respects except scheduling. So far, scheduling has received little attention from workers interested in male reproductive success, but the relevant parameters are generally accessible through direct observation. We encourage more studies.

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