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EVOLUTIONARY OPTIONS FOR MAXIMIZING POLLEN DISPERSAL OF ANIMAL-POLLINATED PLANTS

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In a theoretical analysis of gender allocation in hermaphroditic plants, Lloyd concluded that "intrasexual selection to increase the proficiency of pollen donation, particularly *the number of visitors that can remove pollen from a flower,* is the major selective force guiding floral evolution" (1984, p. 300, emphasis in the original; see also Willson and Price 1977; Udovic 1981; Charnov 1982; Sutherland and Delph 1984; Bell 1985; Stanton et al. 1986). Selection for improved paternal fitness could result in a variety of evolutionary responses because changes in pollen removal, transport, and/or deposition on stigmas could all improve pollen donation. One such response might be to produce more pollen, which should generally result in a plant siring more seeds. However, if the resources devoted to reproduction are limited, this increased allocation of resources to male function could occur at the expense of female function (Charnov 1979; Charlesworth and Charlesworth 1981; Lloyd 1984). Alternatively, a plant's success as a father could depend on its temporal deployment of pollen (Thomson and Barrett 1981; Lloyd and Yates 1982), because some allocations of pollen among pollinators may reduce the uncertainty of successful pollen transport, thereby promoting pollen dispersal to stigmas.

Plants can distribute pollen among pollinators by either packaging or dispensing mechanisms (Lloyd and Yates 1982). Packaging is the division of a plant's total pollen production into separate units (packages), which sequentially become available to pollinators. For example, any plant that staggers either anthesis within an inflorescence or anther dehiscence within a flower is engaged in packaging (for a survey, see Percival 1955). In contrast, dispensing mechanisms restrict the amount of available pollen that a pollinator removes from a package during a single flower visit (see Lloyd and Yates 1982; Brantjes 1983). For example, in the Campanulaceae, anthers shed pollen onto the outer surface of the style, where it is held in place by retractable hairs: retraction proceeds gradually along the style, thereby restricting pollen removal by individual pollinators (Lloyd and Yates 1982). Packaging and dispensing are not exclusive and may operate simulta-

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neously as in *Lupinus* (Dunn 1956) and *Lobelia* (Devlin and Stephenson 1985), both of which have acropetal inflorescences and control removal of pollen from individual flowers.

In this paper, we ask what patterns of pollen packaging and dispensing maximize the number of pollen grains reaching the stigmas of other plants. The mechanics of pollen removal and transport by a pollinator determine the functional relation between pollen removal and deposition that governs pollen dispersal. We therefore begin our analysis by describing pollen transport for two lily species (*Erythronium americanum* Ker and *E. grandiflorum* Pursh). On the basis of these results, we then develop a general model of pollen transport to determine the most effective means of packaging and dispensing pollen. To consider some of the ecological influences on maximizing pollen dispersal, our models incorporate different patterns of pollen removal during a series of flower visits and limited pollinator availability. Finally, we interpret the function of a variety of floral characters with respect to their potential role in maximizing pollen dispersal.

METHODS

Pollen Removal

Measuring pollen removal during a flower visit requires an estimate of the amount of pollen available before the visit. To estimate pollen availability we employed one of two statistical descriptions of pollen production. *Erythronium* flowers produce six large anthers in two whorls. The anthers in each whorl dehisce relatively synchronously, but the outer whorl generally dehisces 1 day before the inner whorl. Pollen production by a flower's inner anthers is highly correlated with production by its outer anthers (*E. americanum*, log-transformed data, $r = 0.947$, $N = 48$, $p < 0.001$; Harder et al. 1985). In addition, an individual anther's pollen production is highly correlated with the anther's length before dehiscence (*E. grandiflorum*, log-transformed data, $r = 0.902$, $N = 40$, $p < 0.001$). The second relation enables the use of flowers with some or all anthers fully dehisced (*E. grandiflorum* experiments), whereas the use of the first relation requires that only the outer three anthers can be dehisced (*E. americanum* experiments).

To measure pollen removal, we allowed a bee to visit a fresh flower with three or six fully dehisced anthers. After the visit, dehisced anthers were collected and preserved in 70% ethanol until the remaining pollen could be counted with a Coulter Counter® (model TAII; for further details, see Harder et al. 1985). We then estimated the amount of pollen removed by the bee by subtracting the count of the pollen left by the bee from the flower's predicted pollen availability. The length of each bee visit was timed with a stopwatch to the nearest 0.1 s.

We also measured the number of pollen grains falling beneath an *E. americanum* flower during a bee visit. These experiments were conducted in a small screen cage (30 cm × 30 cm × 30 cm), and individual flowers were held over a clean sheet of paper during the bee visit. After the visit, pollen was scraped from the paper with a glass microscope slide and then washed from the slide into a vial until it could be counted under a microscope.

Pollen Deposition

Our procedures for measuring pollen deposition, which employed the natural pollen dichromism found in *E. grandiflorum*, are described fully elsewhere (Thomson and Plowright 1980; Thomson 1986; Thomson et al. 1986; Thomson and Thomson, in press). Briefly, we brought flowers with red pollen into large flowering stands that included only flowers with yellow pollen near Kebler Pass, Colorado. A chilled bumble bee queen (*Bombus occidentalis*) was then allowed to warm up and begin feeding on a bouquet of yellow-pollen flowers. Once she could fly, the bee was induced to visit the red-pollen donor with three or six dehisced anthers. After following the bee at a distance and marking the next 20–40 flowers visited, we collected the stigmas of recipient flowers. These stigmas were then examined microscopically to count the number of red pollen grains, all of which must have been brought there from the donor by the observed bee. Although *E. grandiflorum* is self-compatible, we considered only grains exported to other flowers in determining the total pollen deposition realized by a donor flower. For each donor flower, we also measured pollen removal as described above, to establish the relation between removal and total deposition. Essentially all pollen deposition from a particular donor occurs during the next 20 flower visits (Thomson et al. 1986).

RESULTS

Pollen Removal and Deposition for 'Erythronium'

Nectar-collecting queen bumble bees (*Bombus ternarius* and *B. terricola*) and worker honey bees (*Apis mellifera*) removed up to 87.9% of the pollen available on dehisced anthers of *Erythronium americanum* during a single flower visit (fig. 1). The number of pollen grains removed (R) depended on the number available (A_0) and the amount of time the bee spent on the flower (L); thus,

$$\hat{R} = 0.772 A_0 (1 - e^{-0.071L})$$

($r^2 = 0.819$, $p < 0.001$) or, alternatively,

$$\hat{P} = 0.772\,(1 - e^{-0.071L}),$$

where P is the proportion of available pollen removed. For these flowers, the estimated average (± SD) pollen availability was 41,500 ± 13,410 grains. Bees removed pollen quite rapidly during short visits (and presumably during the beginning of longer visits), but their overall removal rate declined with increasing visit duration as the proportion removed approached an average asymptote of 0.772. The bee species did not differ in their pollen-removal efficiency.

On the average (± SD), 14.0% ± 8.31% of the pollen removed from a flower fell to the ground and was not carried away by the bee. As with pollen removal, the amount of fallen pollen (F) increased with the duration of the flower visit (fig. 2; $\hat{F} = 426.7\,T^{0.625}$, $r^2 = 0.616$, $N = 29$, $p < 0.001$). However, multiple-regression results indicate that the amount of pollen removed did not explain a significant

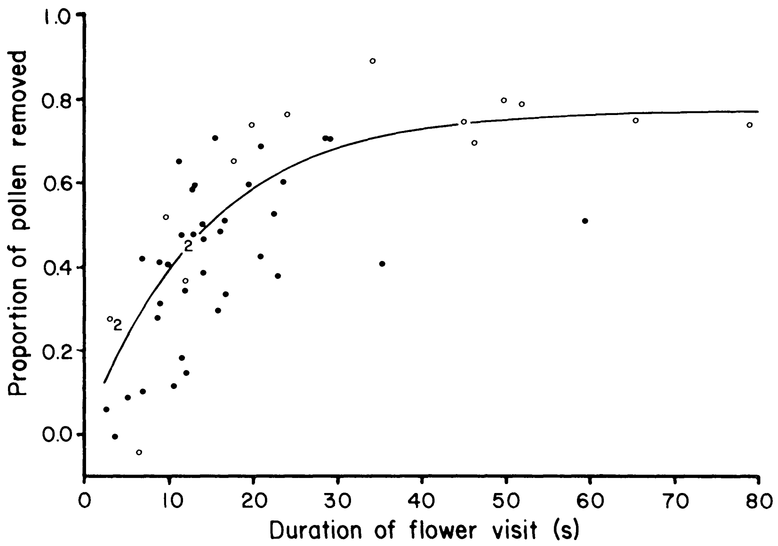

FIG. 1.—The proportion of available pollen removed from *Erythronium americanum* flowers in relation to the length of the visit by the pollinator: *solid symbols*, bumble bee queens; *open symbols*, honey bee workers.

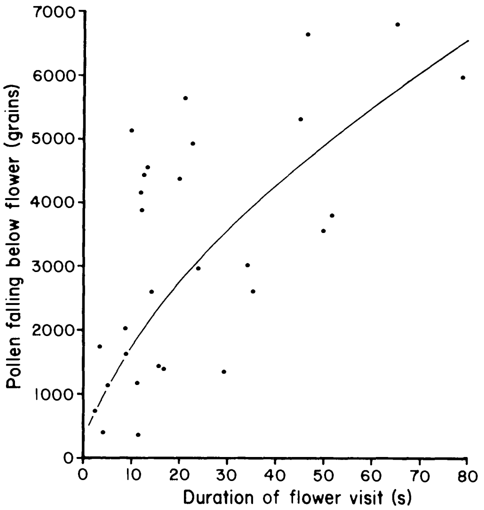

FIG. 2.—Amount of pollen falling beneath *Erythronium americanum* flowers during a bee visit in relation to the length of the visit.

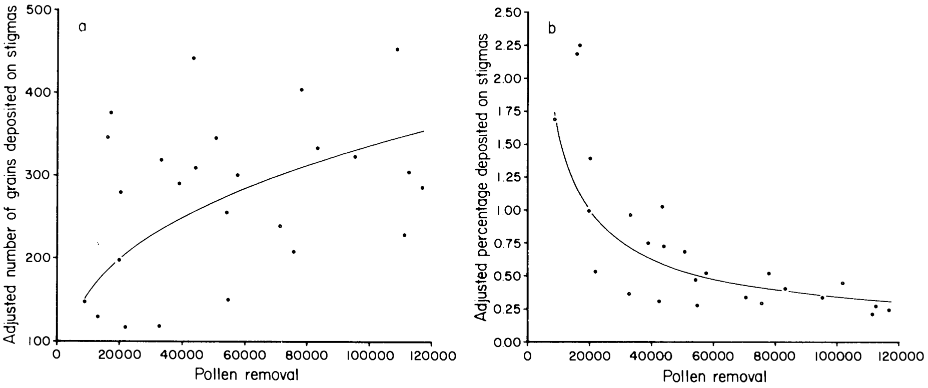

FIG. 3.—The relation between the pollen removal from 25 donor *Erythronium grandiflorum* flowers and subsequent deposition on stigmas of the next 20 recipient flowers visited by *Bombus occidentalis* queens. *a*, The number of grains deposited; *b*, the percentage of removed pollen deposited. To facilitate presentation, the residuals around the complete multiple-regression equation have been plotted as though each donor flower received the average 158 self grains. *b*, The prediction line is based on the regression statistics estimated from the data in *a*.

portion of the remaining variation in the amount of fallen pollen once the effect of the duration of the visit had been removed ($p > 0.5$).

Bees visiting *E. grandiflorum* deposited an average of only 0.6% of the pollen that they removed from a particular donor flower on stigmas of the next 20 recipient flowers (fig. 3). The number of pollen grains deposited on stigmas of recipient flowers (D) varied with the number of grains removed from the donor (R) and the number of grains deposited on the donating flower's stigma (S, for self pollen),

$$\hat{D} = R^{0.329} S^{0.403} \tag{1}$$

(fig. 3*a*; coefficient of determination $R^2 = 0.612$ for log-transformed data, $N = 25$, $p < 0.001$). The relation between self- and outcrossed-pollen deposition suggests that when pollen was deposited on the bee's body so as to result in considerable self-pollination, it was also more favorably located for deposition on the stigmas of subsequently visited flowers. Because the partial-regression coefficient associated with the amount of pollen removed is significantly less than 1 ($s_b = 0.045$, $t = 14.98$, $p < 0.001$), pollen deposition is a decelerating function of removal.

Maximizing Pollen Deposition with Unlimited Pollinators

Having determined that pollen dispersal by a single pollinator is an increasing, but decelerating, function of pollen removal (fig. 3; eq. 1), we can begin to model a plant's total pollen dispersal. We assume that pollen is always deposited on a similar location on the pollinators' bodies, so that equation (1) can be generalized to

$$D = aR^g . \tag{2}$$

In this equation, the constants a and g reflect the loss of the pollen leaving a donor plant during its dispersal to recipient flowers, and we refer to them collectively as the attenuation coefficients. This attenuation results from passive loss, such as pollen falling beneath the flower during removal (fig. 2), and active loss resulting from pollinator grooming.

In addition to the relation between pollen removal and deposition by a single pollinator (eq. 2), total pollen dispersal from a particular plant depends on the number of pollen-removing visits and on the amount of pollen each pollinator removes. In modeling pollen dispersal, we initially assume unlimited pollinator availability before considering two more-realistic conditions: a limited, but fixed, number of visits; and an uncertain number of visits with a specified mean. During the course of these visits, successive pollinators could remove pollen in various patterns. Our models contrast two possible removal patterns: the situation in which each pollinator removes the same number of pollen grains during a flower visit (numerical removal); and removal of a fixed proportion of available pollen (proportional removal). These patterns do not exhaust the range of alternatives, but incorporating them in the models illustrates that the removal pattern can influence the particular packaging and dispensing strategies needed to maximize pollen dispersal.

Numerical removal.—Consider a single pollen package that initially contains A_0 pollen grains. If each pollinator removes R pollen grains, then the maximum number of visits (V) during which pollen can be removed from that package is

$$V = A_0/R \tag{3}$$

(fig. 4*a*, *dotted curve*). Total deposition (T) of pollen removed by all pollinators is given by the product of equations (2) and (3),

$$T = aR^{g-1}A_0 . \tag{4}$$

Total deposition declines with increasing pollen removal (fig. 4*b*, *dotted curve*), because when g is less than 1, as it is for *Erythronium* (fig. 3*a*), the proportion of removed pollen that an individual pollinator deposits on stigmas (aR^{g-1}) declines as the number of grains removed increases (fig. 3*b*). Consequently, when pollinators are unlimited, a plant would maximize its total dispersal of pollen to stigmas if each animal removed only a single pollen grain.

Proportional removal.—When each pollen vector removes the same proportion (P) of the available pollen, pollen availability (A_v) after v visits is

$$A_v = A_0 (1 - P)^v ,$$

where A_0 is the pollen availability before any pollinator visits. Because this function has an asymptote of zero, it is necessary to define an "empty" flower as one containing some small number of pollen grains. It follows that the number of visits required to empty a flower of all but A_V pollen grains is

$$V = (\log A_V - \log A_0)/\log(1 - P) ,$$

which is a declining function of P (fig. 4*c*, *dotted curve*). The number of pollen grains removed during the vth visit is

$$R = A_0(1 - P)^{v-1}P . \tag{5}$$

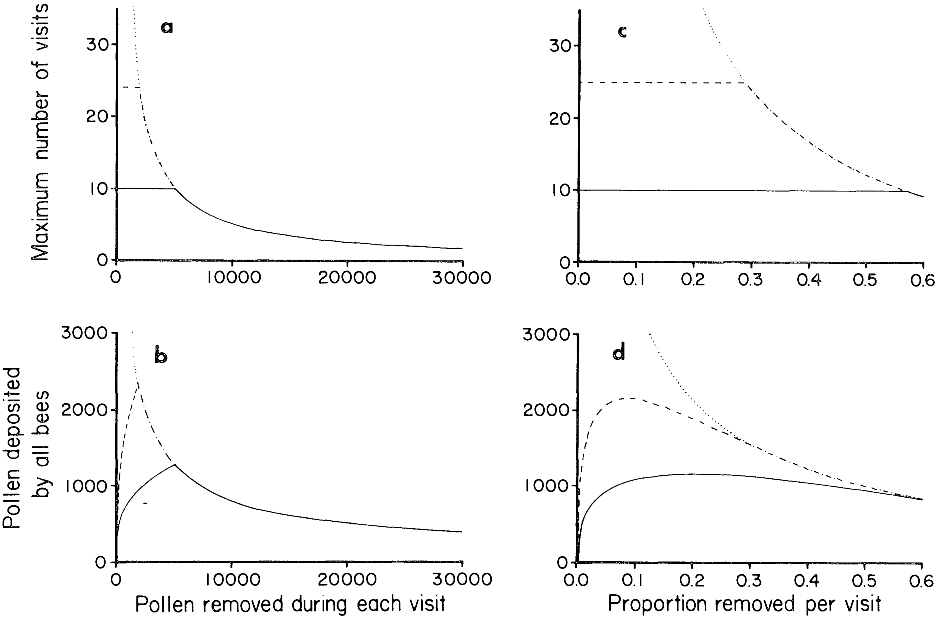

FIG. 4.—Dependence of the maximum number of pollen-removing visits to a pollen-donating donor plant (*a*, *c*) and the total number of grains deposited on recipient stigmas by all pollen-removing visitors (*b*, *d*) on the intensity of numerical (*a*, *b*) and proportional (*c*, *d*) pollen removal. *Solid lines*, The effect of a maximum of 10 visits; *dashed lines*, a maximum of 25 visits; *dotted lines*, unlimited pollinator availability. $A_0 = 50{,}000$ grains, $a = 7.7$, $g = 0.33$. A flower was considered "empty" when only 10 pollen grains remained.

Combining equations (2) and (5) gives the expected number of pollen grains deposited as a result of the vth pollen-removing visit,

$$D = a[A_0(1 - P)^{v-1}P]^g .$$

Summing the deposition resulting from V visits gives the total number of grains deposited for a given level of proportional removal:

$$T = \sum_{v=1}^{V} a[A_0(1 - P)^{v-1}P]^g ,$$

a finite geometric series that simplifies to

$$T = a(A_0P)^g[1 - (1 - P)^{gV}]/[1 - (1 - P)^g] . \qquad (6)$$

As with numerical removal, total deposition is a steadily declining function of the proportion of pollen removed when pollinators are unlimited, as long as $g < 1$ (fig. 4*d*, *dotted line*). Again, total pollen deposition is maximized by restricting the amount of pollen removed by each pollinator as much as possible.

Dispensing Strategies Given Limited Pollinator Availability

Numerical removal.—Because pollen vastly outnumbers pollinators, the extreme limitation of pollen removal suggested by equation (4) is unrealistic, even if it were physically possible. In fact, individual flowers frequently receive few pollinator visits (Feinsinger 1978; Augspurger 1980; Paton and Ford 1983; Motten 1986; Sih and Baltus 1987). To examine the impact of different dispensing strategies on pollen dispersal when pollinator availability is limited, assume that a single pollen package receives a fixed number of pollinator visits (V_L). As long as all of these visits do not remove the available pollen ($V_L R < A_0$), total pollen deposition,

$$T = aR^g V_L \,, \tag{7}$$

increases with increasing removal (fig. 4*a*, *dashed* and *solid lines*). When each pollinator removes enough pollen (R^*) that the V_L visits are just sufficient to remove all of the available pollen, total pollen deposition is maximized and equation (4) equals equation (7) (fig. 4*b*, *dashed* and *solid lines*), so that

$$R^* = A_0/V_L \,. \tag{8}$$

Hence, the amount of pollen removed per pollinator that maximizes total deposition by all pollinators depends only on the initial pollen availability and the fixed number of pollinator visits. This deposition-maximizing pollen removal is not affected by the rate of pollen loss during dispersal, because coefficients a and g do not appear in equation (8). In contrast, the rate of pollen loss does influence the maximum possible pollen deposition (T^*) for a fixed number of pollinator visits,

$$T^* = aA_0^g V_L^{1-g} \,, \tag{9}$$

which is found by substituting R^* from equation (8) into equation (7). A decrease in pollinator availability increases the level of pollen removal required to maximize total deposition, but the number of pollen grains reaching stigmas declines (fig. 4*b*, *dashed* and *solid lines*).

Proportional removal.—With proportional removal, as with numerical removal, the maximum number of pollen-removing visits equals the number of available pollinators (V_L), as long as each visitor removes a sufficiently small proportion (P) of pollen that the V_L visits do not empty the anthers (fig. 4*c*, *dashed* and *solid lines*). For proportional removal, however, total pollen deposition (eq. 6) does not increase monotonically with removal for a fixed number of visits. Setting the first derivative of equation (6) with respect to P equal to zero and solving for P gives the proportional pollen removal that maximizes total pollen deposition (P^*):

$$\begin{gathered} P^* V_L[1 - (1 - P^*)^g] \\ - [1 - P^* - (1 - P^*)^g][1 - (1 - P^*)^{-gV_L}] = 0 \,. \end{gathered} \tag{10}$$

Although this equation does not have a direct solution, only the fixed number of visits (V_L) and the attenuation coefficient g should influence P^*. Hence, optimal proportional removal differs from optimal numerical removal by depending on the rate of pollen loss but not on original pollen availability (A_0; see eq. 8). Because total pollen deposition (eq. 6) does not increase monotonically with P, it can be maximized even though pollen remains undispersed (approximately 10% of total production for the cases illustrated in fig. 4*d*).

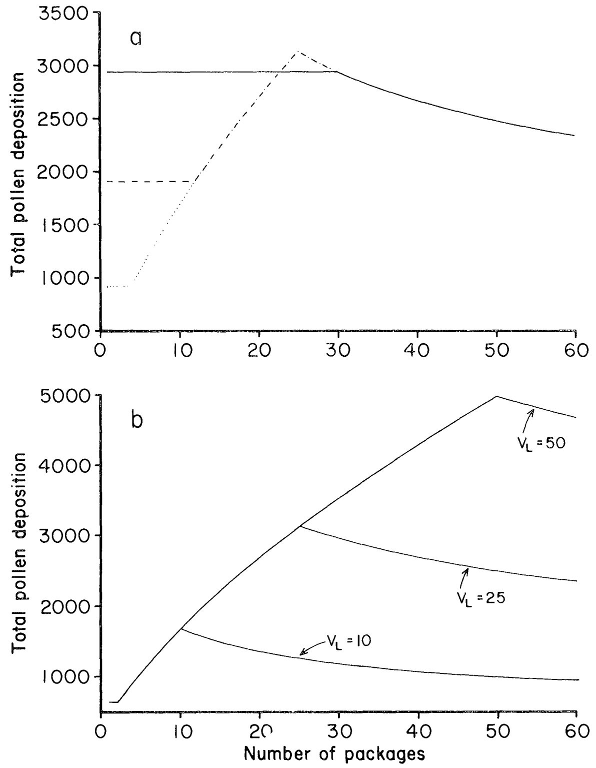

FIG. 5.—The relation between the number of pollen packages and total pollen deposition for numerical removal. *a*, The effect of different levels of potential removal during each of 25 flower visits ($V_t = 25$; *solid line*, $R = 4000$ grains; *dashed line*, $R = 10{,}000$ grains; *dotted line*, $R = 30{,}000$ grains); *b*, the dependence of pollen deposition on the number of available pollinators ($R = 50{,}000$ grains). For both panels, total pollen production (A_t) is 120,000 grains, $a = 7.7$, and $g = 0.33$.

Packaging Strategies Given Limited Pollinator Availability

Numerical removal.—Consider now the effect on total pollen dispersal of breaking a plant's total pollen production (A_t) into n packages. We assume that only the A_0 grains ($A_0 = A_t/n$) from a single package are available at any time and that equation (7) describes the dependence of pollen deposition on pollen removal and pollinator availability. During a plant's flowering period, it receives V_t flower visits, which are regularly distributed in time; each package therefore receives $V_L = V_t/n$ visits, on the average. In considering packaging alternatives, we further assume either that each pollinator removes R grains if they are available or that the package is emptied if fewer than R grains remain.

Pollen availability (A_0) and the amount of pollen each pollinator can remove (R) interact to determine three possible relations between total pollen deposition (T_t) and the number of packages (fig. 5*a*). First, when a single visit does not empty a package ($A_0 > R$) and there are too few pollinators to empty a package during its life ($V_L R < A_0$), the number of packages does not affect total deposition from all packages:

$$T_t = naR^g V_L = aR^g V_t$$

(fig. 5*a*, horizontal portions of all curves). Second, when each visit empties a package ($A_0 \leq R$) and there are more pollinators than packages ($V_t > n$), total deposition,

$$T_t = naA_0^g = aA_t^g n^{1-g}, \tag{11}$$

increases with the number of packages, because increased packaging restricts pollen removal by each pollinator and increases the number of pollinators moving pollen (fig. 5*a*, ascending portions of dashed and dotted curves). Finally, total pollen deposition,

$$T_t = aA_0^g V_t = aA_t^g V_t/n^g, \tag{12}$$

declines as the number of packages increases when each visit empties a package ($A_0 < R$) and there are more packages than pollinators ($V_t < n$), because pollen in unvisited packages remains undispersed (fig. 5*a*, descending portions of all curves).

These different relations between total pollen deposition and the number of pollen packages produce two different expectations for the degree of packaging required to maximize pollen dispersal. When a plant receives too few visits to remove all of the pollen produced, regardless of the number of packages ($RV_t \leq A_t$), no single number of packages maximizes total deposition of pollen on stigmas (fig. 5*a*, *solid line*). Because the total cost to the plant of packaging pollen probably increases with the number of packages, producing a single package would be the most efficient deployment. In contrast, when all pollinators can remove a plant's total pollen production ($RV_t > A_t$), total deposition is maximized when the number of packages equals the total number of available pollinators,

$$n^* = V_t \tag{13}$$

(fig. 5*a*, *dashed* and *dotted lines*; fig. 5*b*), a result that is independent of the amount of pollen removed, the rate of pollen loss, and total pollen production. Substituting n^* into equation (11) provides the maximum possible pollen deposition (T_t^*),

$$T_t^* = aA_t^g V_t^{1-g},$$

which is identical to the maximum pollen deposition for dispensing with numerical removal (eq. 9). This identity obtains because packaging restricts actual pollen removal by each pollinator to A_0/V_L grains, which is the optimal level (R^*; eq. 8) for dispensing.

Proportional removal.—Pollen dispersal from n packages following V_t visits during which pollinators remove a fixed proportion (P) of the pollen remaining in each package can be found by altering equation (6). When visits (V_t) outnumber packages (n), deposition from an individual package (T) is

$$T = a(A_t P)^g [1 - (1 - P)^{gV_L}]/n^g [1 - (1 - P)^g]; \tag{14}$$

and total deposition from all packages (T_t) is given by

$$T_t = n^{1-g}a(A_tP)^g[1 - (1 - P)^{gV_L}]/[1 - (1 - P)^g], \tag{15}$$

which reduces to equation (11) when $P = 1$ ($V_L = V_t/n$). When there are fewer packages than pollinators, each visited package receives a single visit if visits are regularly distributed ($V_L = 1$ for visited packages). For visited packages, equation (14) then simplifies to

$$T = a(A_tP)^g/n^g,$$

and equation (15) becomes

$$T_t = V_ta(A_tP)^g/n^g, \tag{16}$$

which reduces to equation (12) when $P = 1$. Because the function described by equation (16) declines monotonically with increasing n, total pollen deposition must be maximized with respect to n when pollinators outnumber pollen packages. Setting the first derivative of equation (15) equal to zero gives

$$\ln[1 - gV_t\ln(1 - P)/n^*(1 - g)] + gV_t\ln(1 - P)/n^* = 0. \tag{17}$$

Although this equation has no direct solution, the optimal number of packages (n^*) depends only on the proportion of pollen removed by each pollinator (P; fig. 6*a*), the total number of pollinator visits (V_t; fig. 6*b*), and the attenuation coefficient g.

Variation in Pollinator Availability

To this point, we have treated pollinator availability for a given situation as a constant. In contrast, plants experience variable numbers of pollinator visits (see, e.g., Schemske et al. 1978; Willson and Bertin 1979; Sih and Baltus 1987; Kato 1988). The effect of this variation on dispensing and packaging can be examined by treating the number of visits that a package receives as a random variable. For example, for dispensing with numerical removal, optimal removal is found by modifying equation (8) to

$$\mathrm{E}(R^*) = A_t \sum_{v=0}^{\infty} q_v(1/v), \tag{18}$$

and equation (9) to

$$\mathrm{E}(T^*) = aA_t^g \sum_{v=0}^{\infty} q_v v^{1-g}, \tag{19}$$

where E( ) is the expected value (mean) of the quantity in parentheses, and q_v is the proportion of plants receiving v visits. We consider only the effect of uncertain pollinator visits on optimal dispensing, because the general conclusions for packaging and dispensing are similar.

Two alternatives exist for the likelihood that a particular plant will be visited: all plants have an equal probability of visitation; or some plants are more likely to

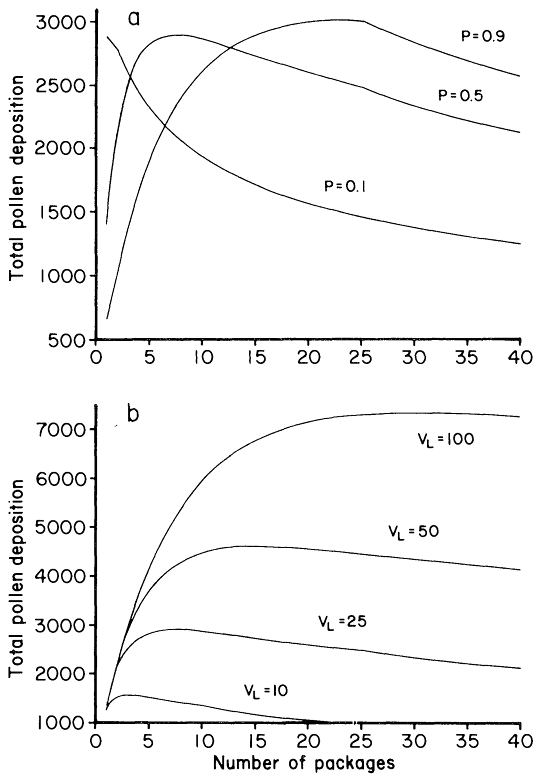

FIG. 6.—The relation between the number of pollen packages and total pollen deposition for proportional removal. *a*, The effect of different levels of removal during each of 25 flower visits ($V_t = 25$); *b*, the dependence of pollen deposition on the number of available pollinators ($P = 0.5$). For both panels, total pollen production (A_t) is 120,000 grains, $a = 7.7$, and $g = 0.33$.

be visited than others. These alternatives can be respectively represented by Poisson and negative-binomial distributions for q_V. Because the solutions to equations (18) and (19) (numerical removal) and the stochastic form of equation (6) (proportional removal) are analytically complex for these distributions, we have solved these equations numerically.

Figure 7 contrasts the effects of a fixed frequency of pollinator visits (deterministic curve) with an equal probability of visits (Poisson curve) and an unequal probability of visits (curves associated with values of k, the parameter of the negative-binomial distribution that determines the inequality in visitation probabilities). The impact of variation in the frequency of pollinator visits on the level of pollen removal that maximizes expected total deposition depends on the distribution of visits (fig. 7). For both numerical and proportional removal, an equal probability of visits (Poisson distribution) affects optimal removal most when flowers receive few visits, on the average. In contrast, unequal probabilities of pollinator visits (negative-binomial distribution) influence optimal removal levels

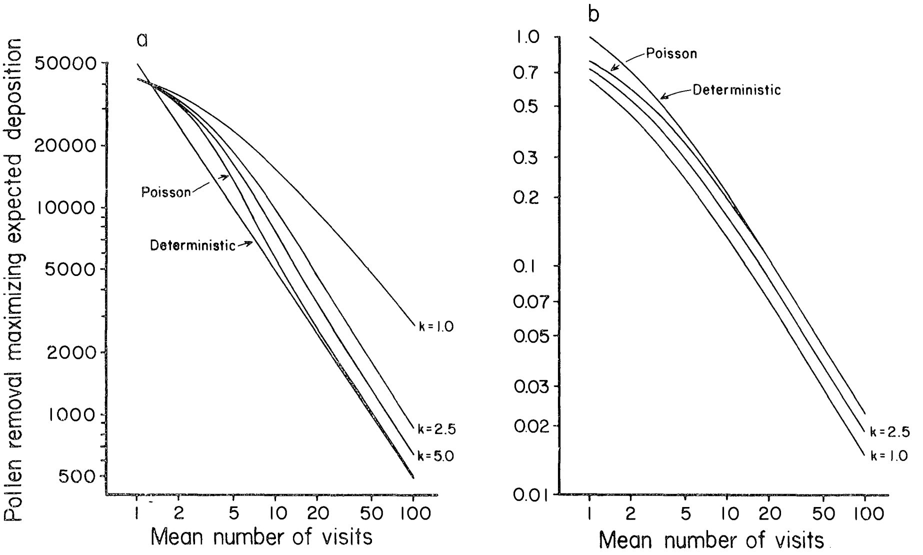

FIG. 7.—The effect of variation in pollinator availability on the level of pollen removal that maximizes expected total deposition of pollen on stigmas: *a*, numerical removal; *b*, proportional removal. The crossover of the stochastic and deterministic models in *a* arises because flowers that received no visits for stochastic distributions with low mean numbers of visits were assumed to offer their total pollen production. Model parameters are as in figure 4.

for even a high expected frequency of visits. This influence increases directly with the disparity in visitation probabilities (i.e., as k decreases; fig. 7).

Although the risk of reduced pollen dispersal associated with stochastic pollinator visits alters the optimal level of pollen removal, the most effective means for dealing with this risk can differ for numerical and proportional removal (figs. 7, 8). To maximize their expected pollen dispersal, plants that experience numerical removal should guard against the likelihood of fewer pollinator visits than average by allowing each pollinator to remove more pollen than would be optimal if the number of visits were certain (fig. 7*a*). This "risk aversion" would also be appropriate for proportional removal if the attenuation coefficient g were between 0.7 and 1 (fig. 8). However, when g is less than 0.6, as it is for *Erythronium* (fig. 3*a*), allowing less pollen removal than is optimal when visits are certain maximizes expected pollen dispersal (figs. 7*b*, 8). This dependence of risk sensitivity on g is not a factor for numerical removal because, unlike proportional removal (eq. 10), optimal removal is not affected by g (see eq. 8).

Regardless of the type of risk sensitivity involved, variation in pollinator visitation depresses the expected number of pollen grains reaching stigmas relative to the donation through a fixed number of visits (fig. 9). Optimal numerical removal results in slightly greater expected pollen deposition than optimal proportional removal for a given mean number of visits. In addition, maximal expected pollen deposition is more sensitive to variation in pollinator availability for proportional removal.

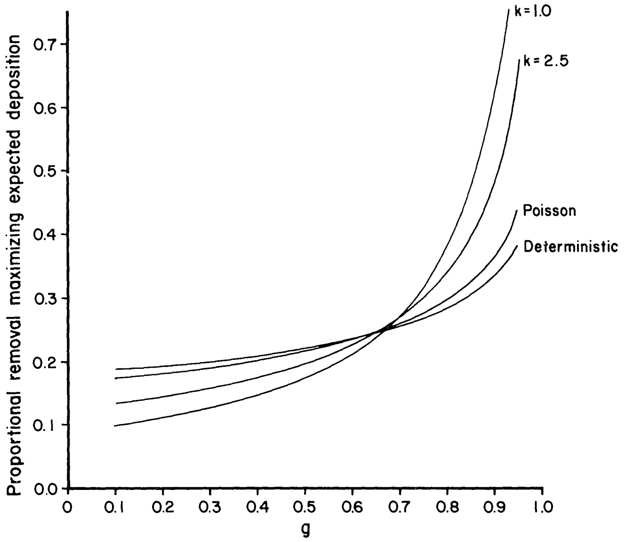

FIG. 8.—Dependence of the optimal level of proportional pollen removal on the attenuation coefficient *g* for different types of variation in pollinator availability. See figure 7 for an explanation of the different curves. The expected number of visits, $E(V_L)$, is 10; other model parameters are as in figure 4.

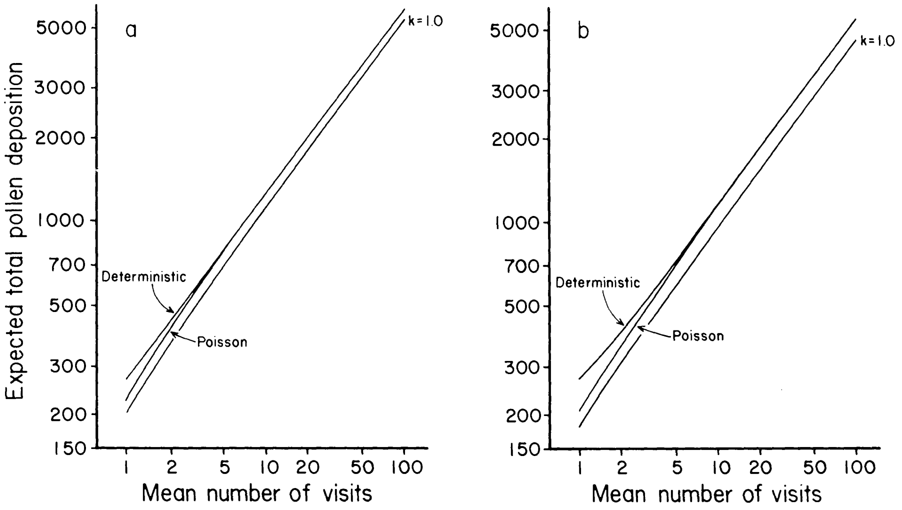

FIG. 9.—The effect of variation in pollinator availability on the expected total deposition of pollen on stigmas following optimal removal: *a*, numerical removal; *b*, proportional removal. See the text for an explanation of the different curves. Model parameters are as in figure 4.

DISCUSSION

Maximizing Pollen Deposition

Plants pay a large price, in terms of lost male gametes, for using animals as sexual proxies. Bees can remove over 80% of the pollen available in a flower during a single visit (fig. 1; Dunham 1939; Strickler 1979); however, only 0.6% of the pollen leaving an *Erythronium* flower arrives on the stigmas of other plants, on the average (fig. 3). Part of this loss occurs when pollen falls directly beneath the flower during the pollinator's visit (fig. 2). The larger component of pollen loss probably results from grooming by the bee while it flies between flowers (Thomson 1986). Levin and Berube (1972) similarly found that *Colias* butterflies deposited only about 0.5% of the pollen removed from *Phlox* flowers on stigmas of subsequently visited plants. Much of the loss of *Phlox* pollen resulted when a butterfly coiled and uncoiled its proboscis.

The returns to a plant, in terms of the proportion of removed pollen that reaches stigmas, diminish as the amount of pollen removed increases (fig. 3*b*). Therefore, a plant could generally maximize pollen dispersal by limiting the pollen removed by individual pollinators (see also Lloyd and Yates 1982), given the constraints imposed by the expected number of pollinator visits (figs. 4, 5*b*, 6*b*, 7). Effective dispensing and/or packaging strategies should allow all of the pollinators visiting a plant to participate in pollen dispersal, while ensuring the removal of most of the pollen produced by the time flowering finishes.

These general conclusions do not depend on whether each pollinator removes the same number or the same proportion of pollen grains, but the removal pattern does affect specific features of the optimal level of pollen removal, whether it is achieved through dispensing or packaging mechanisms. Optimal numerical removal depends on pollen production and on the expected number of pollinator visits (eqs. 8, 13). Optimal proportional removal likewise depends on pollinator availability, but it is not influenced by pollen production and does depend on the attenuation coefficient g (eqs. 10, 17). Following optimal numerical removal, all of the plant's pollen should have been removed (figs. 4*b*, 5): optimal proportional removal leaves a small amount of pollen in the anthers (figs. 4*d*, 6).

The removal pattern also affects the variety of optimal packaging strategies for a given pollinator availability. Changing numerical removal results in an abrupt shift between two optimal numbers of packages (fig. 5*a*). If all of the pollinators visiting a plant cannot remove the available pollen, a single package would be most economical; otherwise, the number of packages should equal the number of pollinators (eq. 13). In contrast, the number of packages needed to maximize pollen dispersal for proportional removal increases continuously with the proportion of pollen removed by each pollinator (fig. 6*a*).

Unfortunately, the removal pattern is not known for any plant, and the biological relevance of these differences is therefore unclear. In all likelihood, neither numerical nor proportional removal adequately represents the removal pattern for most plants. Orchids (Orchidaceae) and milkweeds (*Asclepias*) may be exceptions because they produce pollen in pollinia rather than as discrete grains, and their pollinators therefore probably remove roughly the same number of grains during any flower visit.

Floral Mechanisms Restricting Pollen Removal

Most plants probably possess mechanisms that reduce pollen removal by individual pollinators during a single visit. Pollen packaging is the most obvious mechanism, but it can be implemented in surprisingly subtle forms. A plant's total pollen production can be hierarchically divided into inflorescences, individual flowers, stamens, and even anther sacs. Pollen may be presented sequentially within all of these organizational levels, as in bristly sarsaparilla, *Aralia hispida* (Thomson et al., in press), or within some subset. Percival (1955) collected data on pollen presentation by 81 Welsh species, which clearly illustrate the prevalence of packaging. She found that anthers did not dehisce simultaneously or in the bud in 52 species: in 44.2% of the species, anthers dehisced over more than 1 day within a flower or inflorescence, as in *Erythronium*.

Dispensing may be less common than packaging among angiosperms, but the diversity of mechanisms employed is considerably greater. Percival (1965) recognized four categories of pollen presentation that can be characterized as dispensing mechanisms: secondary pollen presentation, as seen in lupines (*Lupinus*; Dunn 1956), Campanulaceae (Lloyd and Yates 1982; Brantjes 1983), and Asteraceae; gradual opening of an anther from one end to the other (*Erythronium*); contraction of the anther, squeezing pollen out of terminal pores (*Rhododendron*); and anthers lodged under tension in separate pockets in the corolla, such that each stamen must be "tripped" to remove its pollen (*Kalmia*). To this list can be added poricidal anthers, which limit pollinator access to pollen, require specialized pollinator behavior for pollen removal (see, e.g., Buchmann 1983; Snow and Roubik 1987), and release pollen over a protracted period (Buchmann et al. 1977; Goodwin 1986). Poricidal anthers are known in 6%–8% of angiosperm species in at least 72 families (Buchmann 1983). Each of these features restricts the amount of available pollen removed during a single pollinator visit and could enhance the number of pollen grains reaching stigmas from a given donor.

Nectar production provides plants with a nonstructural mechanism for dispensing pollen. Figure 1 illustrates that the amount of pollen removed from *Erythronium americanum* flowers by nectar-feeding bees depends on the duration of the flower visit. Because the time that nectar-collecting pollinators spend on a flower depends on the volume and viscosity of nectar ingested (Montgomerie 1984; May 1985; Pivnick and McNeil 1985; Harder 1986; Tamm and Gass 1986), plants could indirectly control pollen removal by controlling nectar production (for an unusual nectar mechanism that limits visit duration and increases the number of visits a flower receives, see Whitham 1977).

The relation between nectar availability and pollen removal enables testing the general prediction that an intermediate level of pollen removal maximizes pollen deposition. Such a test would require first manipulating the nectar content of donor flowers with marked pollen to alter pollen removal and then measuring pollen dispersal. Unfortunately, natural pollen dichromism, as seen in *Erythro-*

nium, is rare, and marking techniques (review in Handel 1983) are generally inappropriate when both removal and deposition must be measured. Electrophoretic markers can be profitably employed to measure a donor plant's paternal contribution to seed production by neighboring recipient plants (Handel 1983). However, variation in paternity could result from aspects of reproduction other than pollen dispersal, including gametophytic competition and incompatibility.

Uncertainty of Pollinator Visits

Disparity between plants in the probability of being visited alters the level of pollen removal required to maximize expected deposition (fig. 7). Several aspects of the natural history of plants could result in unequal probabilities of pollinator visitation. First, plants are often spatially aggregated, such that individuals tend to be either more closely associated or more isolated than is characteristic of random dispersion. Because pollinators typically move between closely neighboring plants (Waddington and Heinrich 1981), isolated plants can receive considerably fewer visits than aggregated individuals (Thomson 1981; Sih and Baltus 1987; but see Schmitt 1983*a*). Second, forest herbs that are pollinated by heterothermic insects are especially subject to disparities in the frequency of pollinator visits, depending on the amount of time they experience full sunlight (Beattie 1971). Third, plants that flower early in the species' flowering period typically receive fewer visits than later-flowering plants, apparently because of a lag in assessment of new resources by pollinators (Barrett 1980; Thomson 1980, 1981, 1982; Gross and Werner 1983; Schmitt 1983*a*,*b*; Sih and Baltus 1987). Finally, variable weather that altered pollinator activity during a species' flowering period would also induce heterogeneous visitation probabilities (Teräs 1976*a*,*b*; Schemske 1977).

Given this diversity of influences on pollinator behavior, unequal visitation probabilities are probably common. On the basis of our analysis of the effects of uncertain pollinator visits on optimal dispensing strategies (figs. 7, 8, 9), this uncertainty alters the restriction of pollen removal that will maximize expected total pollen deposition. However, the evolutionary change in pollen removal required to alleviate the risk of reduced pollen dispersal may depend on both plant and pollinator characteristics. Given unequal probabilities of pollinator visitation between individuals, plant species with numerical pollen removal should always allow more pollen removal per visit than would maximize pollen dispersal if pollen visits were certain (fig. 7*a*). For plants with proportional removal, the change in allocation of pollen among pollinators required to maximize expected pollen dispersal depends on the attenuation coefficient g (fig. 8), which probably depends on the frequency and efficiency of pollinator grooming. When the proportion of pollen that pollinators remove scarcely affects the proportion of removed pollen deposited on stigmas (percent deposited), pollen removal per visit should be increased ($g > 0.7$; fig. 8). However, when the percent deposited declines dramatically as the proportion removed increases ($g < 0.6$), plants would maximize expected pollen dispersal by gambling on being visited by more pollinators than average, thereby increasing pollen dispersal by all pollinators (fig. 7*b*). Regardless of the type of risk sensitivity involved, the cost of implementing the appropriate response, in terms of reduced expected pollen deposition, should be relatively small (fig. 9).

The uncertain frequency of pollinator visits places a premium on packaging and dispensing mechanisms that provide flexibility in the amount of pollen removed during a particular visit. This flexibility is easily achieved by allowing pollen presentation to increase through time, independently of the frequency of visits. For example, *Erythronium* anthers dehisce by gradually splitting and everting from base to tip (for similar examples, see Percival 1965). When pollinator visits are frequent, each pollinator encounters anthers that have dehisced only slightly since the preceding visit. In contrast, when pollinators are rare, the anthers dehisce much more between visits, thereby allowing removal of more pollen. The use of nectar to control the duration of pollinator visits also allows pollen removal to be tuned to pollinator availability, as long as nectar continues to accumulate (see, e.g., Kato 1988; Thomson et al., in press). In addition to these dispensing mechanisms, packaging generally provides flexible presentation, because pollinator visits do not seem to affect anthesis or anther dehiscence directly.

By comparison, mechanisms that dispense a relatively fixed amount of pollen do not allow such facultative changes in pollen dispersal. For example, in *Lupinus* the stigma is pushed through the massed pollen in the tip of the keel petal, and each pollinator receives a "stigma-full" of pollen on its abdomen (Dunn 1956). This floral mechanism probably does not allow for increased pollen removal during periods of low pollinator availability. Relatively inflexible dispensing mechanisms such as this should be most common in frequently visited species, because they would experience a proportionately smaller reduction in total pollen dispersal (fig. 9).

Constraints on Restricting Pollen Removal

Evolution of the restricted pollen removal predicted by our models could be subject to three types of limitations: phylogenetic constraints; costs associated with packaging and dispensing; and conflicts between restricting pollen removal and maintaining other aspects of floral function. Of these, phylogenetic constraints may be the least influential because pollen removal can be restricted by many alternative mechanisms. We have demonstrated for numerical removal that optimal dispensing and optimal packaging result in the same success in pollen dispersal. In addition, we have outlined the diversity of mechanisms for packaging and dispensing pollen, which provide many alternatives for restricting pollen removal. As a consequence, there are probably many evolutionary solutions to selection for enhanced pollen dispersal.

Physiological costs of producing and maintaining many pollen packages could constrain particular packaging strategies, because the total cost to a plant of producing perianths and support structures is probably greater for many small packages than for a few large packages (see Chaplin and Walker 1982). Because this acceleration in costs with increased packaging tends to counteract the associated gross benefits, the optimal number of packages will be smaller than suggested by equations (13) and (17). Packaging may often be combined with dispensing mechanisms to overcome this limitation.

Restriction of pollen removal to improve pollen dispersal could coincidentally conflict with two other aspects of floral function, pollinator attraction and pollen receipt. Both dispensing and packaging tend to lower a pollen-collecting bee's foraging efficiency per flower, thereby decreasing the plant's attractiveness. If these bees are the plant's main pollinators, maintaining attractiveness may necessitate fewer packages and/or greater pollen removal per visit. Restricting pollen removal by limiting nectar production would similarly reduce a plant's attractiveness to nectar-foraging pollinators, although the relation between nectar concentration and viscosity may alleviate this constraint. Changes in nectar concentration below about 40% sucrose (mass of solute per mass of solution; Montgomerie 1984; May 1985; Pivnick and McNeil 1985; Harder 1986; Tamm and Gass 1986) have little effect on ingestion rates of nectarivorous animals, because viscosity increases rather gradually with concentration in that range. Hence, a plant could restrict the length of a flower visit and still provide the pollinator with an acceptable rate of energy intake by providing a small volume of fairly concentrated nectar.

Deposition of pollen on stigmas also depends on the length of a flower visit (Thomson and Plowright 1980; Thomson 1986); thus, restricting nectar availability to limit pollen removal could also limit pollen receipt for a hermaphroditic flower. Separating male and female function in time (dichogamy) would avoid this conflict by allowing different levels of nectar production by a flower in the male or female phase. Dichogamous flowers for which seed production is pollen-limited should therefore produce nectar more slowly in the male phase. This pattern has been frequently observed (Pyke 1978; Best and Bierzychudek 1982; Cruden et al. 1983; Galen and Plowright 1985; but see Bell et al. 1984), but corresponding information on pollinator limitation of seed production has not been reported. Devlin and Stephenson (1985) found the opposite pattern in *Lobelia cardinalis*, which is not pollen-limited (Devlin and Stephenson 1987).

The requirements of female function should have little effect on selection to enhance male function when seed production is resource-limited. On the basis of a model of the relative durations of male and female phases for dichogamous flowers, Lloyd and Yates (1982) concluded that sexual selection should lengthen the male phase only when pollen availability does not limit seed production. This longer male phase allows more pollinator visits per flower and could increase pollen dispersal if it were accompanied by selection to restrict pollen removal per pollinator (fig. 9).

The arrival of a pollen grain on a conspecific stigma does not ensure pollen-tube growth, fertilization, or production of viable seed. Consequently, the proportion of pollen grains fertilizing ovules must be even less than the 0.5%–0.6% observed for *Erythronium grandiflorum* (fig. 3*b*) and *Phlox* (Levin and Berube 1972). Despite this additional loss of pollen, the evolutionary improvement of dispensing and packaging, along with reduction in the effectiveness of pollinator grooming, would enhance overall paternal fitness, because most pollen loss occurs during transport.

SUMMARY

On the average, nectar-collecting bumble bees deposited 0.6% of the pollen removed from the flowers of *Erythronium grandiflorum* (Liliaceae) onto the stigmas of subsequently visited flowers. Because the proportion deposited declined as the amount removed increased, an individual plant would maximize its total pollen dispersal by relying on many pollen-removing visits while limiting the pollen removed by each pollinator. This restriction of pollen removal could be achieved by a plant presenting only a small portion of its pollen at one time (packaging) and/or by limiting the amount of presented pollen that a pollinator removes during a single visit (dispensing). The restriction of pollen removal required to maximize the expected total deposition on stigmas depends on the number of pollinator visits a plant receives, variation in the frequency of visits, and the pattern of pollen removal during a series of visits. Many aspects of floral biology contribute to a plant's ability to restrict pollen removal, including inflorescence size, flower morphology, anthesis patterns, nectar production, and dichogamy. Selection increasing paternal fitness of animal-pollinated plants could therefore elicit one of a variety of evolutionary responses; the specific response will depend on characteristics of both the plant and the pollinator.

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LITERATURE CITED

Augspurger, C. K. 1980. Mass-flowering of the tropical shrub (*Hybanthus prunifolius*): influences on pollinator attraction and movement. Evolution 34:475–488.

Barrett, S. C. H. 1980. Sexual reproduction in *Eichhornia crassipes* (water hyacinth). II. Seed production in natural populations. J. Appl. Ecol. 17:113–124.

Beattie, A. J. 1971. Itinerant pollinators in a forest. Madroño 21:120–124.

Bell, G. 1985. On the function of flowers. Proc. R. Soc. Lond. B, Biol. Sci. 224:223–265.

Bell, G., L. Lefebvre, L.-A. Giraldeau, and D. Weary. 1984. Partial preference of insects for the male flowers of an annual herb. Oecologia (Berl.) 64:287–294.

Best, L. S., and P. Bierzychudek. 1982. Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. Evolution 36:70–79.

Brantjes, N. B. M. 1983. Regulated pollen issue in *Isotoma*, Campanulaceae, and evolution of secondary pollen presentation. Acta Bot. Neerl. 32:213–222.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. Pages 73–113 *in* C. E. Jones and J. R. Little, eds. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Buchmann, S. L., C. E. Jones, and L. J. Colin. 1977. Vibratile pollination of *Solanum douglasii* and *S. xanti* (Solanaceae) in southern California. Wasmann J. Biol. 35:1–25.

Chaplin, S. J., and J. L. Walker. 1982. Constraints and adaptive significance of floral display of a forest milkweed. Ecology 63:1857–1870.

Charlesworth, D., and B. Charlesworth. 1981. Allocation of resources to male and female functions in hermaphrodites. Biol. J. Linn. Soc. 15:57–74.

Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. Proc. Natl. Acad. Sci. USA 76:2480–2484.

———. 1982. The theory of sex allocation. Princeton University Press, Princeton, N.J.

Cruden, R. W., S. M. Hermann, and S. Peterson. 1983. Patterns of nectar production and plant-pollinator coevolution. Pages 80–125 *in* B. Bentley and T. S. Elias, eds. The biology of nectaries. Columbia University Press, New York.

Devlin, B., and A. G. Stephenson. 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. Am. J. Bot. 72:303–310.

———. 1987. Sexual variation among plants of a perfect-flowered species. Am. Nat. 130:199–218.

Dunham, W. E. 1939. Collecting red clover pollen by honeybees. J. Econ. Entomol. 32:668–670.

Dunn, D. B. 1956. The breeding system of *Lupinus*, group *Micranthi*. Am. Midl. Nat. 55: 443–472.

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. Ecol. Monogr. 48:269–287.

Galen, C., and R. C. Plowright. 1985. Contrasting movement patterns of nectar-collecting and pollen-collecting bumble bees (*Bombus terricola*) on fireweed (*Chamaenerion angustifolium*) inflorescences. Ecol. Entomol. 10:9–17.

Goodwin, R. M. 1986. Kiwifruit flowers: anther dehiscence and daily collection of pollen by honey bees. N.Z. J. Exp. Agric. 14:449–452.

Gross, R. S., and P. A. Werner. 1983. Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). Ecol. Monogr. 53:95–117.

Handel, S. N. 1983. Pollination ecology, plant population structure, and gene flow. Pages 163–211 *in* L. Real, ed. Pollination biology. Academic Press, New York.

Harder, L. D. 1986. Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia (Berl.) 69:309–315.

Harder, L. D., J. D. Thomson, M. B. Cruzan, and R. S. Unnasch. 1985. Sexual reproduction and variation in floral morphology in an ephemeral vernal lily, *Erythronium americanum*. Oecologia (Berl.) 67:286–291.

Kato, M. 1988. Bumblebee visits to *Impatiens* spp.: pattern and efficiency. Oecologia (Berl.) 76: 364–370.

Levin, D. A., and D. E. Berube. 1972. *Phlox* and *Colias*: the efficiency of a pollination system. Evolution 26:242–250.

Lloyd, D. G. 1984. Gender allocations in outcrossing cosexual plants. Pages 277–300 *in* R. Dirzo and J. Sarukhán, eds. Perspectives on plant population ecology. Sinauer, Sunderland, Mass.

Lloyd, D. G., and J. M. A. Yates. 1982. Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). Evolution 36:903–913.

May, P. G. 1985. Nectar uptake rates and optimal nectar concentrations of two butterfly species. Oecologia (Berl.) 66:381–386.

Montgomerie, R. D. 1984. Nectar extraction by hummingbirds: response to different floral characters. Oecologia (Berl.) 63:229–236.

Motten, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecol. Monogr. 56:21–42.

Paton, D. C., and H. A. Ford. 1983. The influences of plant characteristics and honeyeater size on levels of pollination in Australian plants. Pages 235–248 *in* C. E. Jones and J. R. Little, eds. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Percival, M. S. 1955. The presentation of pollen in certain angiosperms and its collection by *Apis mellifera*. New Phytol. 54:353–368.

———. 1965. Floral biology. Pergamon, Oxford.

Pivnick, K. A., and J. N. McNeil. 1985. Effects of nectar concentration on butterfly feeding: measured feeding rates for *Thymelicus lineola* (Lepidoptera: Hesperiidae) and a general feeding model for adult Lepidoptera. Oecologia (Berl.) 66:226–237.

Pyke, G. H. 1978. Optimal foraging in bumblebees and coevolution with their plants. Oecologia (Berl.) 36:281–293.

Schemske, D. W. 1977. Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). Bull. Torrey Bot. Club 104:254–263.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59:351–366.

Schmitt, J. 1983*a*. Flowering plant density and pollinator visitation in *Senecio*. Oecologia (Berl.) 60:97–102.

———. 1983*b*. Density-dependent pollinator foraging, flowering phenology, and temporal pollen dispersal patterns in *Linanthus bicolor*. Evolution 37:1247–1257.

Sih, A., and M.-S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology 68:1679–1690.

Snow, A. A., and D. W. Roubik. 1987. Pollen deposition and removal by bees visiting two tree species in Panama. Biotropica 19:57–63.

Stanton, M. L., A. A. Snow, and S. N. Handel. 1986. Floral evolution: attractiveness to pollinators increases male fitness. Science (Wash., D.C.) 232:1625–1627.

Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. Ecology 60:998–1009.

Sutherland, S., and L. F. Delph. 1984. On the importance of male fitness in plants: patterns of fruit-set. Ecology 65:1093–1104.

Tamm, S., and C. L. Gass. 1986. Energy intake rates and nectar concentration preferences by hummingbirds. Oecologia (Berl.) 70:20–23.

Teräs, I. 1976*a*. Bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), on red clover in South Savo, Finland. Ann. Agric. Fenn. 15:116–127.

———. 1976*b*. Flower visits of bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), during one summer. Ann. Zool. Fenn. 13:200–232.

Thomson, J. D. 1980. Skewed flowering distributions and pollinator attraction. Ecology 61:572–579.

———. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. J. Anim. Ecol. 50:49–59.

———. 1982. Patterns of visitation by animal pollinators. Oikos 39:241–250.

———. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. J. Ecol. 74:329–341.

Thomson, J. D., and S. C. H. Barrett. 1981. Temporal variation of gender in *Aralia hispida* Vent. (Araliaceae). Evolution 35:1094–1107.

Thomson, J. D., and R. C. Plowright. 1980. Pollen carryover, nectar rewards, and pollinator behavior with special reference to *Diervilla lonicera*. Oecologia (Berl.) 46:68–74.

Thomson, J. D., and B. A. Thomson. In press. Dispersal of *Erythronium grandiflorum* pollen by bumble bees: implications for gene flow and reproductive success. Evolution.

Thomson, J. D., M. V. Price, N. M. Waser, and D. A. Stratton. 1986. Comparative studies of pollen and fluorescent dye transport by bumble bees visiting *Erythronium grandiflorum*. Oecologia (Berl.) 69:561–566.

Thomson, J. D., M. A. McKenna, and M. B. Cruzan. In press. Temporal patterns of nectar and pollen production in *Aralia hispida*: implications for reproductive success. Ecology.

Udovic, D. 1981. Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. Oecologia (Berl.) 48:389–399.

Waddington, K. D., and B. Heinrich. 1981. Patterns of movement and floral choice by foraging bees. Pages 215–230 *in* A. C. Kamil and T. D. Sargent, eds. Foraging behavior. Garland STPM Press, New York.

Whitham, T. G. 1977. Coevolution of foraging in *Bombus* and nectar dispensing in *Chilopsis*: a last dreg theory. Science (Wash., D.C.) 197:593–596.

Willson, M. F., and R. I. Bertin. 1979. Flower-visitors, nectar production, and inflorescence size of *Asclepias syriaca*. Can. J. Bot. 57:1380–1388.

Willson, M. F., and P. W. Price. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). Evolution 31:495–511.