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Pollen Carryover, Nectar Rewards, and Pollinator Behavior with Special Reference to *Diervilla lonicera*

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Summary. Pollen carryover was measured in three species of bumble bee pollinated plants by counting the numbers of foreign grains applied to the stigmas of a series of flowers by bumble bees. Deposition declined with the number of flowers visited in a roughly exponential fashion; most grains were deposited on the first few flowers, but some grains went much farther, the maximum carryover being 54 flowers. Variation in deposition was very high. In *Diervilla lonicera*, bees desposited significantly more grains on flowers which contained large amounts of nectar than on drained flowers. The implications are discussed in terms of plant strategies for optimizing pollination.

Introduction

The extent of pollen carryover affects important processes in the fertilization of entomophilous plants, e.g., neighborhood size and genetic isolation of strains (Levin and Kerster, 1967, 1968; Levin and Berube, 1972), assortative mating (Kiang, 1972; Levin, 1970), the relative effectiveness of different pollinators (Primack and Silander, 1975; Motten et al., 1979), competition between plants for pollinators (Levin and Anderson, 1970; Straw, 1972; Waser, 1978a, b; Thomson, 1978, 1980), optimal nectar secretion (Hartling, 1979; Hartling and Plowright, 1979), optimal inflorescence architecture (Pyke, 1978), optimal mate selection (Janzen, 1977), and, of course, seed set in many-flowered self incompatible plants (Hartling, 1979; Frankie et al., 1976) and the ratio of selfed to outcrossed seed in self compatible plants (Bateman, 1956; Harding, 1977). It has hitherto usually been assumed that carryover is low, i.e., that pollen picked up at one plant gets no farther than the next plant (Levin and Kerster, 1969) or even the next flower (Frankie et al., 1976). However, the evidence for such assumptions is limited to a small number of studies, mostly by Levin and his colleagues. The recent empirical demonstration by Hartling (1979; Hartling and Plowright 1979) that pollen carryover is unexpectedly high in *Trifolium pratense* suggests that more cases should be examined before accepting low carryover as a general phenomenon. We present additional data for three plant species.

While the functional form of pollen carryover is of most immediate interest, the flower-to-flower variation in grain deposition is also of practical and theoretical importance, as an indicator of pollination reliability. Furthermore, the existence of this variation suggests hypotheses regarding the factors which cause more grains to be deposited in one visit than another. One such hypothesis, examined empirically below, is that a positive correlation exists between the volume of nectar in a flower and the number of grains placed on its stigma. Such a relationship would have obvious implications for the evolution of reward rates of flowers, but to our knowledge has not been suggested before.

Methods and Materials

Three species of bumble bee-pollinated flowers were examined: *Erythronium americanum*, *Clintonia borealis*, (both Liliaceae), and *Diervilla lonicera* (Caprifoliaceae). All were locally common in areas near our study site in central New Brunswick. During May–July 1979, we collected foraging bumble bees and large numbers of flowers and buds, and brought them to the laboratory where the bees were refrigerated and the flowers held indoors in water pending use in pollen deposition trials, which were conducted outdoors, in screened enclosures. The exact procedures employed varied with plant species as follows:

1. In *Erythronium americanum*, we made use of a striking dimorphism in pollen color. Most populations had a majority of yellow-pollen forms with a minority of deep red-pollen individuals. The usefulness of this dimorphism is that red grains may be easily counted against the light background of the stigma. Thus, by introducing a single red flower into a bee's foraging sequence, and examining successively visited yellow flowers, the extent and functional form of *pollen carryover* can be assessed.

For these experiments we used *Bombus* and *Psithyrus* queens which had been caught in areas dominated by yellow-pollen flowers. Bees were examined microscopically to insure that they were carrying no red pollen before their first trials. We placed the chilled bees on a bouquet of yellow-pollen flowers in the screened enclosure. Most began nectar feeding as soon as they had warmed sufficiently. Some did not forage, or foraged only briefly before taking flight and buzzing about the enclosure. These bees were allowed to fly to deplete their energy reserves, then captured, chilled, and again given the opportunity to forage. We found it easier to induce foraging by warming up chilled bees on the flowers than when already warmed bees were introduced. After a bee was warmed up enough to make short flights, we induced it to switch from the warming-up bouquet to a rectangular array of 50 experimental flowers in water vials, spaced ~8 cm apart. Forty-nine of these were yellow-pollen flowers, most of which had indehiscent anthers, although the corollas were fully

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open, stigmas were receptive, and nectar secretion was underway. One freshly dehiscent, previously unvisited red-pollen flower served as a donor. After one bee visit to this flower, we removed it from the array; similarly, we removed all the yellow flowers visited subsequently, preserving them in order of visitation.

The bees usually flew between successive flowers, although occasionally two flowers were close enough, because of the inclination of their scapes, for bees to walk between them, which the bees usually did when possible. Many flights were not to nearest neighbors. Some flights included small circles around the array, and some bees broke off foraging to fly around the enclosure. We held individual flowers from the array, or the array itself, near these bees in an attempt to reinduce foraging. If this was successful, the run was continued; if foraging did not resume after ∼1 min, we stopped the run. The stigmas were then examined and red grains counted.

2. *Clintonia borealis* is similar to *E. americanum* in size, general floral morphology, and extent of protogyny. However, our runs on *Clintonia* differed in several details from those described above. First, because no pollen-color dimorphism exists, we used emasculated receptor flowers. We allowed the bee to become loaded with pollen on the warming-up bouquet of dehiscent flowers before beginning to visit the sequence of cleanstigma, emasculated flowers; thus, we were effectively measuring the carryover of a "bee-load" of pollen rather than the contribution of a single flower as above. Also, we abandoned the flower array, and instead permitted the bees to forage on single, handheld flowers. We presented a new flower next to the one at which the bee was feeding. Usually the bee walked to the next profered flower and began to feed. Because *Clintonia* pollen grains do not contrast with stigmatic backgrounds, we removed the grains for counting by dipping the stigma into blobs of basic fuchsinstained glycerine jelly (Beattie, 1971) which had been melted in place on a microscope slide. Three blobs, 3–4 mm in diameter, were placed on each slide. The stigma was pressed into each of them in a known order, so that absence of grains in the third blob served as a rough check on the completeness of removal. A cover slip was then melted in place and the grains counted under the compound microscope. By applying known numbers of grains to stigmas we verified that the technique was quite accurate as long as careful preparations were made immediately after grain deposition. Even within 1/2 h, pollen tube growth begins to anchor the viable grains to the stigmatic surface, making the procedure unreliable.

3. Carryover runs on *Diervilla lonicera* were carried out as for *Clintonia*, except that flowers were kept separate so that pollinators had to fly between them. In addition to runs with unaltered flowers similar to those above (hereafter called "straight" runs), we conducted "enrichment" runs in which a bee alternated visits between flowers which had been recently (<20 min) drained of nectar and flowers which had been nectar-enriched. Flowers were emasculated before anther dehiscence and chosen for use when they were approximately old enough that dehiscence would have started if the anthers had been intact. Flowers were drained by inserting a 2 µl capillary tube (Drummond Microcaps®) into the nectar spur. Enrichment was achieved by returning 2 µl of nectar (supplemented where necessary by 2/3 M sucrose solution) to the nectar spurs. Two µl of nectar represents a high, but not unnaturally high, volume, based on a small sample of nectar volumes from untampered flowers (see Results). Thus the resulting population was composed of equal numbers of two flower types: enriched flowers with 2 µl of nectar, representing the richest flowers a field-foraging bee would likely encounter, and drained flowers with only residual traces of nectar.

Results

Erythronium

The data from 7 runs on *Erythronium*, comprising 6 individual bees, are summarized in Table 1. It is apparent that most red grains are either deposited on stigmas or lost from the active pool on the pollinator within the first 10–15 flowers, although grains may be deposited sporadically on subsequent flowers, the longest carryover being 54 flowers. There is also substantial variation in the number of grains deposited on successive flowers: three-fold differences occur several times. Direct observations of foragers on both this species and *Clintonia* suggest that the variation is due in large measure to imprecision in the pollen placement process. The stigma was contacted most often by latero-ventral portions of the abdomen, but, depending on the postures adopted by the bees, such contact was completely absent from many apparently successful foraging visits. Another common mechanism of pollen donation was for the stigma to be brushed by the inner angle of a leg joint, usually the tibio-femoral joint of the middle or hind leg, as the bee moved on the flower. Whether this occurred also depended completely on specific movements by the bee.

While the variation seen in Table 1 is an important result in itself, the general form of the pollen carryover curve is also of interest. Figure 1 shows the results of a smoothing attempt; within each of the four *Bombus* runs which contained 18 or more flowers (runs A, B, E and F), the numbers of grains per flower were standardized by dividing by the total number of grains deposited on the first 18 flowers of the run. For each flower sequence position, the mean of the four runs was computed; then a three-point rolling average was taken of the means. The logarithms of these rolling averages are plotted as a function of flower se-

Table 1. Transport of (red) pollen grains from one flower of *Erythronium americanum*. Values in body of table are numbers of grains

Run:	Sequence numbers of receiving flowers:																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30–53	54	55–60
A.	4	6	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0														
B.	14	11	2	5	5	0	3	3	2	0	5	0	0	3	0	1	1	2	0	0	0	0	1	0	1	0	0	0	1	all 0	3	all 0
C.	8	15	3	4	5	3																										
D.	4	0	6	7	3	2	6	0	0																							
E.	5	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	1														
F.	4	7	3	3	5	1	7	0	0	0	0	0	0	1	0	1	1	0														
G.	0	3	0	4	1	0	0	0																								

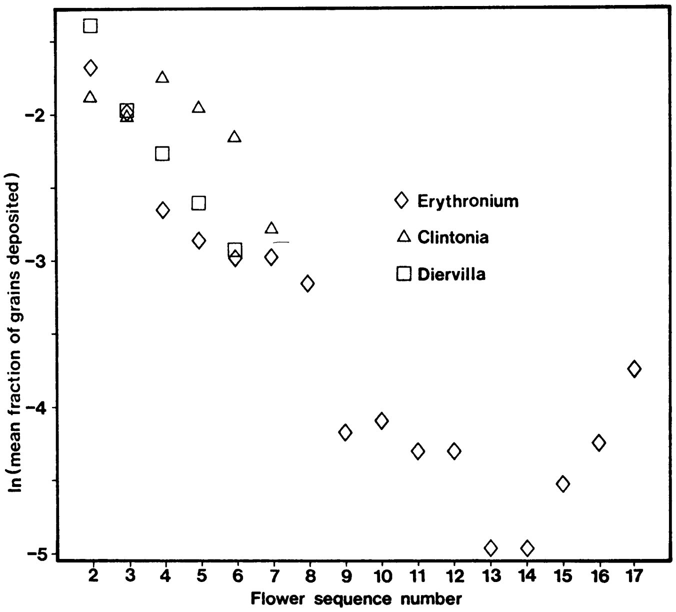

Fig. 1. Pollen carryover curves for the three species *Erythronium americanum*, *Clintonia borealis*, and *Diervilla lonicera*, combined and smoothed as described in the text

Table 2. Transport of a "bee-load" of pollen from *Clintonia borealis* flowers. Values in body of table are numbers of grains deposited

Run:	Sequence numbers of receiving flowers:											
	1	2	3	4	5	6	7	8	9	10	11	12
A.	369	148	110	2								
B.	30	21	153	28	484	12	17	159				
C.	24	21	58	47	19	36	2	2	9	1	6	5
D.	258	178	5	28								
E.	346	21	34	73								
F.	131	142	16	68	45	69	51	17	5	22		
G.	97	20	93	54	49	5	34	6				

quence number in Fig. 1. The rise in this curve at sequence position 17 probably represents a chance superimposition of independent peaks in the separate curves, rather than a real upturning of the curve. The fall of the curve appears to be roughly exponential (straight line of negative slope) for the first several flowers, but this rate of drop decreases for subsequent flowers. That is, the log-linear plot gives a bent rather than a straight line.

Clintonia

The results of runs on *Clintonia*, summarized in Table 2, showed the same trends, as might be expected given the morphological similarity of the flowers. The numbers of grains deposited were considerably larger, because bee-loads were counted rather than the contribution of a single distinctive flower, as in *Erythronium*. The variation in numbers deposited on adjacent flowers is very high, the most extreme examples coming from run B.

Table 3. Transport of a "bee-load" of pollen from *Diervilla lonicera* flowers. Values in body of table are numbers of grains.

I. Straight runs, unmanipulated flowers.

Run:	Sequence numbers of receiving flowers:										
	1	2	3	4	5	6	7	8	9	10	11
A.	80	1	1	5	18	2	0	2	0	1	0
B.	48	10	32	12	21	23	11				
C.	24	63	8	8	19	0	4	0	10	1	
D.	32	5	4	8	1	0	3	1			

II. Enrichment runs; enriched flowers denoted by underline

Run:	Sequence numbers of receiving flowers:								
	1	2	3	4	5	6	7	8	9
A.	42	$\underline{129}$	22	$\underline{86}$					
B.	$\underline{90}$	16	$\underline{41}$	7	$\underline{8}$	2	$\underline{0}$	$\underline{4}$	
C.	$\underline{181}$	30	$\underline{69}$	4	$\underline{2}$	3	$\underline{15}$	0	
D.	0	$\underline{2}$	0	$\underline{1}$	0	$\underline{0}$	1	$\underline{4}$	
E.	$\underline{13}$	5	$\underline{0}$	2	$\underline{10}$	0			
F.	34	$\underline{6}$	4	$\underline{12}$	0	0	$\underline{1}$	0	$\underline{1}$

The standardizing, run-combining, and smoothing procedures described above were applied to the first 8 flowers of *Clintonia* runs B, F and G (Fig. 1). The *Erythronium* and *Clintonia* curves are roughly similar, but the *Clintonia* curve drops more slowly. The slopes of least-squares regression lines for the log-linear curves as drawn in Fig. 3 are -0.15 for the 6 *Clintonia* points and -0.28 for the first 6 *Erythronium* points.

Diervilla

The results of 4 "straight" runs (unmanipulated flowers) on *Diervilla* and 6 runs with enriched and drained flowers are shown in Table 3. Variability in grains deposited is again present, although apparently less extreme than in *Clintonia*. There were consistent differences in total deposition between some runs, indicating variation in the initial load carried by the bee. Flower-to-flower variation in deposition in part II of Table 3 appears to be related to nectar level, as evidenced by almost all the drained flowers lying below their enriched neighbors. To test this relationship statistically, we first transformed each number of grains deposited by adding 2 and taking the fourth root. The transformed numbers of grains for the 43 flowers comprised the dependent variable in a multiple regression analysis with three independent dummy variables: run number, flower sequence number, and the enriched or drained character of the flower. The use of dummies allowed these nominal variables to enter the regression equation. Enrichment does indeed explain a significant portion of the variation in transformed grain number ($F_{1,28} = 9.1$, $p < 0.01$). Visual examination of the residuals indicated that the fourth-root transformation was appropriate. Other transformations did not affect the significance of this result. Thus enriched flowers received significantly more grains than drained ones, taking run and

Table 4. Time spent on drained (D) and enriched (E) *Diervilla lonicera* flowers by one *Bombus vagans* worker in a screen-cage trial. Flowers are listed in the order visited. The bee stayed longer on enriched flowers (Mann-Whitney U-test, $p < 0.025$)

Flower type:	E	D	E	E	E	D	E	D	E	D
Time spent (s):	40	18	25	20	18	2	15	4	32	5

Table 5. Nectar volume frequency distributions for two samples of unaltered *Diervilla lonicera* flowers. Sample A: picked 8 July AM, held in water indoors, volume measured 9 July AM. Sample B: picked 13 July PM, measured 14 July AM. Only recently dehisced, unwilted flowers were measured. Values in the body of the table are numbers of flowers

Nectar volume (μl)	0.8 to 1.0	1.0 to 1.2	1.2 to 1.4	1.4 to 1.6	1.6 to 1.8	1.8 to 2.0	2.0 to 2.2	2.2 to 2.4	2.4 to 2.6
Sample A	2	3	1	0	0	0	0	0	0
Sample B	1	1	2	1	2	3	1	0	1

sequence position into account. A bee spent significantly (Mann-Whitney U-test, $p < 0.025$) more time on enriched flowers in a small sample of flowers (Table 4). Table 5 gives nectar volumes from unmanipulated flowers for comparison with the 2 μl volume chosen for enriched flowers. The standardized, combined, and smoothed curve for all *Diervilla* runs except enrichment runs A and E is given in Figure 1. The points fit a straight line well except for a slight bend in the same direction as previously noted for *Erythronium*. The slope of the curve is −0.33, close to that of *Erythronium*.

Discussion

Variation in Grain Deposition – Causes

It would be difficult to discuss the variation in grain deposition per se if bees were allowed to pick up more pollen during the foraging sequence because variation in pollen acquisition by the bee would confound the pattern. In the present experiments the pool of grains on the pollinator must decrease during the run due to deposition, removal by grooming, corbicular packing, and passive loss; thus the observation of one flower receiving 28 grains and the next one receiving 484 (*Clintonia* run B) is strong evidence of an important stochastic component in the transfer from bee to stigma. Although not studied here, it is probable that pollen acquisition – at least in primarily nectarfeeding bees – is equally variable.

All three of the plant species examined have relatively open, campanulate flowers with a strongly exserted style and stamens. It is this openness which allows visitors to miss the stigmatic surface even while reaching to the base of the ovary to obtain nectar. Because the style is long and somewhat flexible, the stigmatic surface is not borne in the same position relative to the nectaries in all flowers; this is especially pronounced in *Diervilla*. Thus, even if all visitors entered in a particular stereotypic manner, some stigmas would be contacted more firmly than others. In fact, nectar-collecting visitors land on and enter these flowers in various ways, most often involving a lateral approach such that the nectaries are often reached initially without touching the stigma. Subsequent movements while on the flower usually involve some stigmatic contact. This is especially true for the *Erythronium* flowers, which were not emasculated. The variation in *Clintonia* deposition was probably higher in these experiments than it would be in non-emasculated flowers; the absence of anthers allowed the bees to extract nectar laterally with less hindrance, and allowed them to penetrate so far inside the flower that their bodies were entirely below the stigma and unlikely to contact it except on leaving. Robinson (1978) describes a similar situation involving untampered flowers. Delicious apples have gaps in the androecium which allow bees to obtain nectar by non-pollinating "sideworking" instead of "topworking", accounting for the low yields commonly found in Delicious strains. Sideworking without fertilization is also well known from other plants, e.g., alfalfa (Reinhardt, 1952). When foraging on normal, open *Clintonia* flowers, *Bombus* queens often use anthers as footholds, which keeps the body farther out of the flower and closer to the stigma. The *Diervilla* flowers were also emasculated and therefore "unnatural" although to a lesser extent because in this case the corolla tube itself (which is intact) has a larger role in guiding foragers; visitors do grasp anthers, but not as often as in *Clintonia*.

It must also be pointed out that all three plant species are protogynous, and the stigma is receptive at or very soon after bud break. Bees will visit flowers before they are fully opened, and the frequency of stigmatic contact is higher at this stage because the stigma is difficult to avoid. Therefore, "poor" visits may be somewhat less common in nature than in our experiments, but such visits undoubtedly do occur. However, even without the variation in placement of plant parts and the variation in animal posture discussed above, the reliability of pollen delivery would still be reduced by variation in the distribution of pollen on bees.

Patchy distribution of pollen on a forager's body could stem directly from patchy placement by the plant donor. Some bee flowers place pollen on specific areas of the body, sometimes so precisely as to help maintain reproduction isolation between congeners (Macior, 1974); however in flowers like *Clintonia*, the variety of approaches to the flower would seem to guarantee a variety of pollen placements. Any particular arrangement of grains on a forager will be further modified by grooming movements, which would most often replace one patchy distribution with another. For example, *Trifolium pratense* (Fabaceae) pollen is apparently applied to a fairly large area of a bumble bee's head, but subsequent grooming removes it from most areas while concentrating the remainder in the proboscidial fossa (Furgala et al., 1960; Spencer-Booth 1965). Such localization on the pollinator may increase the reliability of deposition in flowers such as *Trifolium*, where stigmatic placement is precise, but it will increase the variation in "hit-or-miss" flowers like *Clintonia*.

The rapid disappearance of pollen from the bee's body due to grooming is a major determinant of pollen flow distances. Considering the volume of pollen which passes from their pelage to their corbiculae, even pollen-foraging bees often look surprisingly "clean" while on flowers. This in turn influences the relative rankings of various insects as pollinators. While bumble bees are extraordinarily vigorous in their foraging, it is possible that some generalized flowers might be better served by slower but "dirtier" bees, such as andrenids or megachilids, which carry collected pollen on broad areas of the ventral surface. Motten et al. (1979) compared the pollination efficiency of an andrenid specialist and a bombyliid fly generalist on *Claytonia virginiana* (Portulacaceae), finding them approximately equal except in stands with few dehiscent anthers, where the andrenid was more effective. It would be instructive to compare pollen delivery potential in bumblebees which do or do not groom pollen into corbiculae: e.g., *Bombus vs. Psithyrus* females; *Bombus* females *vs.* males.

Most grooming seems to occur in flight between flowers (Hartling, 1979); since all six legs are involved, grooming while standing is probably less thorough. This could help explain the slower fall-off of pollen carryover in *Clintonia*, where the bees were allowed to walk between flowers, as compared to *Erythronium* and *Diervilla*, where they had to fly.

Plowright and Hartling (in prep.; see also Hartling, 1979) have modeled pollen carryover as a decreasing exponential function. While this appears to fit the observed initial fall-off adequately in all the species, the longer *Erythronium* runs show that the rate of loss slows as more flowers are visited. A plausible explanation is that the frequency or vigor of grooming movements is proportional to the amount of pollen on the body. This makes sense from the standpoint of bee energetics, as well as accounting for the long tail of the deposition curve.

Variation in Grain Deposition – Implications for Plants

Underlying this section is the assumption that selection should operate, especially on the male component of a flower (cf. Janzen, 1977), to reduce the haphazard nature of deposition, and to slow the effective rate of pollen loss from pollinators' bodies. Such selection should favor precise positioning of flower parts and precise guiding of the insect, either by channeling structures or by visual "nectar" guides. The evolution of zygomorphy and hidden nectar in bee flowers may be partly due to this mechanism.

Nectar "hidden" in deep flowers is often considered a result of selection to conceal nectar from some foragers or from the elements. It may, however, have nothing to do with concealment; the significance may be that only one path usually exists to "hidden" nectar (Faegri and van der Pijl, 1979). To channel visitors, a flower need not employ physical barricades, but simply be constructed in such a way that one route to the nectar is quicker or easier than others; the time and energy constraints of foragers will cause them to quickly converge on the "proper" approach (Laverty, 1979; Heinrich, 1979).

When pollen placement on the bee is reliably patchy, either because of predictable pollinator-anther contacts or because of groomed rearrangement, selection should promote precise stigmatic placement, as exemplified by papilionaceous legumes (e.g., Hartling, 1979), Scrophulariaceae (Macior, 1970, 1975; Kwak, 1977), many orchids (e.g., Dressler, 1968; van der Pijl and Dodson, 1966) and other plants. If grooming patterns are predictable, anthers and stigmas need not contact the same areas of the body.

The arguments of the preceding two paragraphs assume that the plants attract only pollinators which are morphologically and behaviorally similar. Plants which utilize various insect pollinators cannot depend on specific morphology or grooming behavior in this manner. The most fundamental tactic would be for anthers and stigmas to be borne in the *same position* relative to nectar (where applicable) so that any forager which acquires pollen on any body part has some likelihood of brushing a similarly-placed stigma with the same part. Such juxtaposition of male and female parts would, however, favor selfing in self-compatible species. Selection for outcrossing could counteract this tendency – without changing the relative positions of the sexual organs – by favoring protandry, protogyny, dioecy, monoecy, and temporal dioecy. Many flowers which attract generalized pollinators employ these tactics; e.g., many composites have protandrous florets arranged in the head such that a ring of female-phase florets surrounds a ring of male-phase florets. A disproportionate number of dioecious plants have small, simple flowers which attract a variety of taxa, e.g., generalist small bees and flies.

Since stigmatic deposition is unreliable in some species, selection could reduce the risk of total failure by producing (or retaining, as a primitive feature) a multiple or branched stylar apparatus with multiple stigmas. Such an arrangement could also increase the number of male mates for the flower (cf. Janzen, 1977), if different stigma lobes were to catch different pollen loads. Because seed-set is important as well as genetic quality, the flower's investment in ovules should be protected by a backup mechanism allowing all ovules to be reached by pollen placed on any one stigma lobe. This is the case in *Medeola virginiana* (Liliaceae) (unpublished notes) and *Aralia hispida* (Araliaceae) (Thomson, Barrett, and Plowright, 1980).

Correlation Between Nectar in Flower and Grains Deposited – Causes

The most apparent explanation for this relation is the greater time spent at enriched flowers (Table 4). Although the bee for which these times were recorded was not foraging at full speed, field observations suggest that the difference in residence times on the two flower types also occurs in faster moving bees. Greater time spent will usually entail more movement. It is possible that, as the main nectar volume is taken up, the remainder is left in clefts which a visitor must shift position to reach (cf. Witham, 1977). In this case, once a bee has begun feeding at a flower, it might be advantageous to drain it completely, whereas if the bee does not encounter nectar on an initial probe, it might be better to leave immediately on the presumption that another forager has recently drained the flower.

Inouye (1976) and Morse (1978) have followed Hawkins (1969) and Hainsworth (1973) to propose that nectar extraction time for bumble bees is nearly instantaneous and therefore negligible. This may not apply to all flowers. Since extraction time was not separated from overall flower handling time in this study, and since only a few times were recorded, it is impossible to make a definite statement about the constancy or negligibility of extraction time. However, the grain deposition data, taken together with the few time data, open the question of extraction time. They furthermore seriously weaken the proposition that all legitimate flower visits are equally valuable, an implicit assumption of most existing logical analyses of the relation between nectar and visitation (e.g., Heinrich and Raven, 1972; Heinrich, 1979; Pyke, 1978; Howell, 1979).

Correlation Between Nectar in Flower and Grains Deposited – Implications

How much nectar should a flower secrete? This question has been most recently reviewed by Heinrich (1979, ch. 11); he proposes that the "correct" amount will be a balance between plant frugality on the one hand and the necessity to obtain pollinator visits on the other. This balance is seen to be complicated by the possibility that selection may sometimes favor "cheaters" – plants which secrete little or no nectar, but which are visited because the presence of rewarding conspecifics keeps the pollinators working despite occasional or even frequent disappointments. Heinrich (1979, pp. 169–170) considers the central question to be one of individual plant anonymity: "If bees were to treat plants of a particular species only as a population and never as individuals, cheater genes could spread, leading to the extinction of that species." He suggests that remote visible (Thorp et al., 1975; also see Kevan, 1975) or olfactory (Heinrich, 1979) discrimination between rewarding flowers and cheaters might enable pollinators to avoid visiting the latter; also that site-specific pollinator foraging would concentrate visits on rewarding flowers. Both these mechanisms would tip the selective balance away from cheating plants. The present findings simplify the existing arguments by providing a direct positive feedback between nectar production and individual plant success. Because of this mechanism, plants with tendencies toward nectar "cheating" would be selected against, and the arguments for optimal nectar secretion rates can be reduced (if simplicity is desired) to simple models involving individual selection (Plowright, Thomson, in prep.) rather than game-theoretical evolutionarily stable strategies and *ad hoc* assumptions regarding remote discrimination, spatial distribution of flowers and the like. "Plant anonymity" disappears. Future work on this topic should aim at integrating the various proposed and demonstrated selective pathways into a theory of the ecology and evolution of nectar secretion.

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References

Bateman, A.J.: Cryptic self-incompatibility in the wallflower: *Cheiranthus cheiri* L. Heredity **10**, 257–61 (1956)

Beattie, A.J.: A technique for the study of insect-borne pollen. Pan Pacif. Ent. **47**, 82 (1971)

Dressler, R.L.: Pollination by euglossine bees. Evolution **22**, 202–210 (1968)

Faegri, K., van der Pijl, L.: The principles of pollination ecology. Oxford: Pergamon Press (1979)

Frankie, G.W., Opler, P.A., Bawa, K.S.: Foraging behaviour of solitary bees: implications for outcrossing of a neotropical tree species. J. Ecol. **64**, 1049–1057 (1976)

Furgala, B., Tucker, K.W.: Holdaway, F.G.: Pollens in the proboscis fossae of honeybees foraging certain legumes. Bee Wld. **41**, 210–213 (1960)

Hainsworth, F.R.: On the tongue of a hummingbird: its role in the rate and energetics of feeding. Comp. Biochem. Physiol. **46A**, 65–78 (1973)

Harding, J., Barnes, K.: Genetics of *Lupinus*. X. Genetic variability, heterozygosity and outcrossing in colonial populations of *Lupinus succulentus*. Evolution **31**, 247–255 (1977)

Hartling, L.K.: An investigation of the relationship between bumble bee foraging behaviour and the pollination of red clover: a component analysis approach. M.Sc. thesis, University of Toronto. pp. 92 (1979)

Hartling, L., Plowright, R.C.: An investigation of inter- and intra-inflorescence visitation rates by bumble bees on red clover with special reference to seed set. Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Sta. Spec. Misc. Publ. **1**, 457–460 (1978)

Hawkins, R.P.: Length of tongue in a honey bee in relation to the pollination of red clover. J. Agric. Sci. Cambr. **73**, 489–493 (1969)

Heinrich, B.: Bumblebee economics. Harvard, Cambridge, Mass. (1979)

Heinrich, B., Raven, P.H.: Energetics and pollination ecology. Science **176**, 597–602 (1972)

Howell, D.J.: Flock foraging in nectar-eating bats: advantages to the bats and to the host plants. Am. Nat. **114**, 23–49 (1979)

Inouye, D.: Resource partitioning and community structure: a study of bumblebees in the Colorado Rocky Mountains. Ph. D. dissertation. University of North Carolina, Chapel Hill (1976)

Janzen, D.H.: A note on optimal mate selection by plants. Am. Nat. **111**, 365–371 (1977)

Kevan, P.G.: Fluorescent nectar. Science **194**, 341–342 (1975)

Kiang, Y.T.: Pollination study in a natural population of *Mimulus guttatus* Dc. Evolution **26**, 308–310 (1972)

Kwak, M.: Pollination ecology of five hemiparasitic, large-flowered Rhinanthoideae with special reference to the pollination behavior of nectar-thieving, short-tongued bumblebees. Acta Bot. Neerl. **26**, 97–107 (1977)

Laverty, T.M.: Flower-visiting behaviour of experienced and inexperienced bumblebees (Hymenoptera: Apidae). M.Sc. dissertation. University of Alberta (1978)

Levin, D.A.: Assortative pollination in *Lythrum*. Amer. J. Bot. **57**, 1–5 (1970)

Levin, D.A., Anderson, W.W.: Competition for pollinators between simultaneously flowering species. Am. Nat. **104**, 455–467 (1970)

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

Levin, D.A., Kerster, H.W.: Natural selection for reproductive isolation in *Phlox*. Evolution **21**, 679–687 (1967)

Levin, D.A., Kerster, H.W.: Local gene dispersal in *Phlox*. Evolution **22**, 130–139 (1968)

Levin, D.A., Kerster, H.W.: Density-dependent gene dispersal in *Liatris*. Am. Nat. **103**, 61–74 (1969)

Macior, L.W.: The pollination ecology of *Pedicularis* in Colorado. Am. J. Bot. **57**, 716–728 (1970)

Macior, L.W.: Behavioral aspects of coadaptations between flower and insect pollinators. Ann. Missouri Bot. Gard. **61**, 760–769 (1974)

Macior, L.W.: The pollination ecology of *Pedicularis* in the Yukon territory. Am. J. Bot. **62**, 1065–1072 (1975)

Motten, A.F., Miller, H.L., Alexander, D.E., Campbell, D.R.: Pollination effectiveness of two insect species visiting the spring wild flower, *Claytonia virginiana*. Abstract in Bull Ecol. Soc. Amer. **60**, 116 (1979)

Morse, D.H.: Foraging rate, foraging position, and worker size in bumble bee workers. In Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Sta. Spec. Misc. Publ. **1**, 447–452 (1978)

Primack, R.B., Silander, J.A.: Measuring the relative importance of different pollinators to plants. Nature **225**, 143–144 (1975)

Pyke, G.H.: Optimal foraging in bumblebees and coevolution with their plants. Oecologia (Berl.) **36**, 281–294 (1978)

Reinhardt, J.F.: Some responses of honey bees to alfalfa flowers. Am. Nat. **86**, 257–275 (1952)

Robinson, W.S.: Influence of 'Delicious' apple blossom morphology on the behavior of nectar-gathering honey bees. In Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Sta. Spec. Misc. Publ. **1**, 393–399 (1978)

Spencer-Booth, Y.: The collection of pollen by bumble bees, and its transportation in the corbiculae and the proboscididial fossa. J. Apic. Res. **4**, 185–190 (1965)

Straw, R.M.: A Markov model for pollinator constancy and competition. Am. Nat. **106**, 597–620 (1972)

Thomson, J.D.: Competition and cooperation in plant-pollinator systems. Ph. D. dissertation. University of Wisconsin-Madison (1978)

Thomson, J.D.: Visitation rate patterns in animal-pollinated plants. Submitted to Ecology (1980)

Thomson, J.D., Barrett, S.C.H., Plowright, R.C.: Reproductive biology of *Aralia hispida* (Araliaceae) II. Behaviour of bumble bee pollinators. In prep. (1980)

Thorp, R.W., Briggs, D.L., Estes, J.R., Erickson, E.H.: Nectar fluorescence under ultraviolet irradiation. Science **189**, 476–478 (1975)

van der Pijl, L., Dodson, C.H.: Orchid flowers, their pollination and evolution. University of Miami Press, Coral Gables, Fla. (1966)

Waser, N.M.: Interspecific pollen transfer and competition between co-occurring plant species. Oecologia (Berl.) **36**, 223–236 (1978a)

Waser, N.M.: Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology **59**, 934–944 (1978b)

Witham, T.G.: Coevolution of foraging in *Bombus* and nectar dispensing in *Chilopsis*: a last dreg theory. Science **197**, 593–595 (1977)

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