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POLLEN TRANSPORT AND DEPOSITION BY BUMBLE BEES IN *ERYTHRONIUM*: INFLUENCES OF FLORAL NECTAR AND BEE GROOMING

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SUMMARY

(1) The transport of pollen from donor flowers by bumble bees was measured by examining deposition on stigmata of sequences of recipient flowers. The rate of decay of grain deposition was estimated as a measure of pollen carryover.

(2) *Bombus bifarius* was a much less effective pollinator of *Erythronium grandiflorum* than was the larger *Bombus occidentalis.*

(3) The numbers of pollen grains deposited by bumble bees on the stigmata of *Erythronium americanum* vary greatly from flower to flower.

(4) The time spent by a bee on a flower is positively related to the nectar concentration and volume.

(5) Flowers with large volumes of nectar receive more pollen grains per visit than those with small volumes, presumably because the visits are longer. The results are insufficient to show a parallel increase in deposition with nectar concentration.

(6) Measures of pollen carryover are presented. Most deposition of grains from a particular donor flower occurs on the first several recipient flowers subsequently visited by the bee, but a few grains travel much farther.

(7) Pollen carryover in *E. grandiflorum* is reduced by bee grooming.

(8) The negative effect of grooming on carryover is increased when the recipient flowers have undehisced anthers.

(9) *Erythronium americanum* and *E. grandiflorum* were similar in carryover, but *Linaria vulgaris* showed much higher carryover. The reasons for this are discussed.

INTRODUCTION

Gross deviations from random mating are commonly observed in populations of flowering plants and restricted transport of pollen by pollinators often contributes strongly to this pattern; see reviews by Levin & Kerster (1974) and Levin (1981). Besides influencing the general mode of plant evolution, the mechanical process of pollen dissemination has been presumed to drive the evolution of many specific characters of plants, such as flower and inflorescence structure, nectar secretion patterns and pollen production. However, there have been relatively few quantitative studies of the process of pollen transport. Studies of lepidopteran pollination systems by Levin and his colleagues (Levin & Kerster 1974; Levin 1981) pointed to extremely limited pollen carryover beyond the first flower visited. Recent work on other systems has found somewhat more extensive pollen transport by bees and hummingbirds (Schaal 1980; Thomson & Plowright 1980; Price & Waser 1982; Waser & Price 1982). This study provides measures of the extent of pollen transfer in bee-pollinated plants, especially of the genus *Erythronium*.

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There are two obstacles to such studies: the methodological problem of tracking pollen grains to measure carryover; and the statistical problem of comparing data sets. The great variety of techniques used to measure pollen dispersal—stains (Linhart 1973), fluorescent dusts (Stockhouse 1976), radiotracers (Schlising & Turpin 1971), neutron activation analysis (Gaudreau & Hardin 1974) and marker genes (Schaal 1980)—suggests that this problem has no universal solution. Only Price & Waser (1982) have attacked the formidable statistical questions. In the *Erythronium* species studied here, a natural pollen-colour dimorphism eliminates the need to mark grains and some alternative statistical procedures are presented. The influences of pollinator grooming behaviour and of the dehisced or undehisced state of the anthers of recipient flowers are examined in *Erythronium grandiflorum* Pursh (Liliaceae). Pollen flow in *E. grandiflorum* is compared to that in a similar congener, *E. americanum* Ker., and to that in the very different *Linaria vulgaris* Mill. (Schrophulariaceae). The effects of variation in nectar content on the deposition of pollen in *Erythronium americanum* are examined.

METHODS

Experimental procedure

Erythronium americanum

This species displays a conspicuous dimorphism in pollen colour in some eastern North American populations. The study stands, near Glassville, western New Brunswick (40°29′N, 74°27′W), have a majority of yellow-pollen forms and a minority of reddish-brown or castaneous pollen forms. When both grain types are intermingled on a stigma, the red grains are easily distinguishable from the yellow under a dissecting microscope. In the experiments described below, nectar-feeding bumble bees (*Bombus ternarius* Say) were induced to visit sequences of cut flowers in an outdoor flight cage. The introduction of individual red-pollen flowers into sequences of yellow-pollen flowers allowed the use of the 'naturally marked' red pollen to determine the extent to which pollen is transported from one flower to succeeding flowers under nearly natural conditions. The general experimental procedure follows that described by Thomson & Plowright (1980).

Bumble-bee queens which are native pollinators of *E. americanum* in New Brunswick, were captured and refrigerated between trials. After a bee had warmed up to flight temperature while feeding from a small bouquet of sucrose-enriched flowers, she would often begin visiting a series of flowers, which were presented in an array of water-filled vials. The vials were positioned so as to force the bee to fly between successive flowers. With a few exceptions, noted below, all the results are from an individual bee. Descriptions of the foraging bouts were tape-recorded, and the time spent on each flower determined. Flowers were removed from the array as soon as they had been visited and were examined, in sequence order, for red grains. Because the stigmata of the flowers always bore unambiguously distinguishable red and yellow grains, it was assumed that these colours were essentially permanent. Later work on *E. grandiflorum* disclosed that some red grains do lose their colour abruptly; this renders them indistinguishable from the yellow grains and is associated with their hydration and germination. This is a gradual process in *Erythronium*; grains in close contact with stigmatic papillae decolour fastest. In the experiments described here and in Thomson & Plowright (1980), all counts were made in the evening of the day of the run. Extrapolation from 'fading rate' trials carried out in this laboratory with *E. grandiflorum* suggests that the numbers of red grains counted under these circumstances are about 30–50% of the real values. Although this technical flaw is unfortunate, the data are still useful for testing a number of hypotheses. Comparisons, of flowers within runs and of decay curves between runs, should be valid even though estimates of absolute grain numbers are not.

Flowers were picked as unopened buds and allowed to open indoors, protected from insect activity. Red- and yellow-pollen flowers were segregated before anther dehiscence to avoid contamination. In several of these experiments, naturally occurring nectar was first removed from the flowers by blotting the nectaries with small filter-paper wicks. Then, known volumes and concentrations of reagent-grade sucrose solutions were added to the flowers using a Hamilton dispensing microsyringe. Four experimental series were run. In type-1 runs, the bee encountered equal numbers of flowers with 12·5, 25 and 50% sucrose solution, the volume being held constant at 2 μl per flower. In type-2 and type-3 runs, nectar volume was varied—1, 2 or 4 μl—and the concentration kept constant. Type-2 runs used 12·5% sucrose; type 3, 25%. In type 4, one-third of the flowers were drained and not replenished; one third contained 3 μl of 25% sucrose in the lowest nectary; and one third contained 1 μl of 25% sucrose in each of the three nectaries. The different treatments were alternated in the array of vials, but it was impossible to force the bees to visit them in order.

Erythronium grandiflorum

This species was used to evaluate the effect of bee grooming on pollen carryover. In 1981, the transfer of *E. grandiflorum* pollen by queens of *Bombus bifarius* Cresson and *Bombus occidentalis* Greene was examined at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. One experiment compared runs with undehisced recipient flowers *v.* runs with dehisced, polleniferous recipients. (*Erythronium grandiflorum* is sufficiently protogynous to ensure that the stigmatic papillae are well developed and receptive for a brief period before anther dehiscence.) Bumble bees usually groom in flight between flowers, but often omit grooming if they simply step from one flower to the next. To introduce variation in pollinator grooming, runs in which bees had to fly between flowers were compared to runs in which they were allowed to walk between flowers. However, it was not possible to suppress all grooming. Bees would break off, in the course of 'walking' runs, to make grooming flights. They could not be prevented from grooming even by wing clipping that rendered them flightless; such bees would either groom while standing or while hanging from a flower by their mandibles. It was therefore necessary to consult the tapes for each run to determine when grooming occurred.

Linaria vulgaris

This species was chosen for comparison with *Erythronium* because its closed, zygomorphic flower and complicated pollination mechanism (Faegri & van der Pijl 1979) suggested that the deposition of pollen on the stigmata might be more precise and reliable than in the open, radially symmetrical flower of *Erythronium*, where deposition is a highly variable, hit-or-miss process (Thomson & Plowright 1980). Since *Linaria* has no pollen-colour dimorphism, it was necessary to emasculate recipient flowers, which can be done easily without impairing the mechanical function of the flower. Experiments were done indoors, at Stony Brook, New York, U.S.A., in August 1981. *Bombus fervidus* workers picked up pollen at a freshly dehiscent donor flower; after visitation, the stigmata of recipient flowers were excised, squashed, and mounted in glycerine jelly tinted with basic fuchsin (Beattie 1971) and all pollen grains counted.

TABLE 1. Mean handling times of three *Bombus ternarius* queens on *Erythronium americanum* flowers with differences in nectar dispersion.

	Flower type					
	Single-pool*			Triple-pool†		
	Time (s)	*n*	S.E.	Time(s)	*n*	S.E.
Bee A ('Blue')	7·06	20	0·89	6·99	16	0·68
Bee B	19·62	5	0·80	21·57	3	5·14
Bee C	16·92	4	4·88	18·25	2	10·95

* 'Single-pool' flowers contained 3 μl of 25% sucrose solution deposited at the base of the bottommost tepal.

† 'Triple-pool' flowers contained 1 μl of 25% sucrose solution deposited at the base of three alternating tepals.

Data analysis

Nectar treatments: Erythronium americanum *and* Bombus ternarius

Analysis of the handling times of bees on flowers with different nectar contents was hampered by between-run variation in working speeds of the bees. This was most obvious when different bees were compared (see Table 1), but also seemed to occur between runs of the single queen 'Blue'. Possible reasons include differences in temperature, in the speed of the bee's recovery from refrigeration and in hunger. Therefore, before combining figures from different runs, each handling time was standardized by dividing it by the mean time for the run. These transformed variates were pooled for all runs of a given type and subjected to a Kruskal–Wallis test for significance of a nectar-treatment effect.

The parallel analysis of pollen deposition data is much more complicated. The results typically show a sharp decline in grain number with flower sequence number. There is great variation between successive flowers; the 'decay curves' are far from smooth. Further, there is great variation between the runs in the total amount of red pollen delivered. In some cases, the bee apparently either picked up very little red pollen at the beginning of the run or groomed most of it off its body before visiting the sequence of recipient flowers.

To determine whether nectar content influences pollen deposition in such a heterogeneous data set, it is necessary to take account of (i) the inherent, roughly exponential decline in grains with each run; (ii) the fact that, once the bee's pool of grains has been exhausted, all flowers must receive zero grains regardless of nectar treatment; and (iii) the heterogeneity among runs. First, the grain-count data were transformed by adding 1 and taking the natural log (so that curvilinear decay could be reasonably well fitted by a linear regression line). Secondly, the sequences were truncated after the last non-zero grain count, thus using only flowers for which it was certain that the visiting bee still carried some red grains. Thirdly, for each run separately, the remaining data points were fitted with a least-squares regression. The residuals were examined to determine whether a given point was above or below the regression line, and the data from all runs of one type were cast into a 2×3 contingency table where each point was cross-classified by the sign of its residual and by its nectar treatment. Thus, if a nectar treatment enhanced deposition relative to others in the run, the grain counts of those flowers should tend to lie above a line fitted through the data. Because the nectar categories could be ordered, nectar effects were tested using a modified χ^2 procedure (Cochrane 1954).

Carryover comparisons

To estimate the extent of pollen carryover in each data set, counts of grains from all succeeding pairs of flowers were considered. The number of grains (G_n) on the flower from sequence position n were plotted against the number of grains (G_{n-1}) on the flower immediately preceding. The aim was to establish a relationship that could be used to write an iterative equation that would predict the pollen decay rates. Because the raw-data scatter diagrams of G_n *v.* G_{n-1} showed excessive clumping near the origin and suggested undue influence on the computed regression line by a smaller number of outliers, the raw data were transformed by adding one and taking the natural logarithm. This increased the correlation in the larger data sets. A least-squares regression line, constrained through the origin, was then fitted to the transformed data. The slope b of this line is the exponent of the equation

$$G_n + 1 = (G_{n-1} + 1)^b,$$

which may be solved iteratively to produce the expected decay curve from a specified initial load of pollen. Thus b is a measure of carryover in this power-law model. When it is small, decay is rapid. One can test for differences in carryover between two data sets 1 and 2 by testing for differences in the regression slopes b, using the F-ratio

$$F_{(1,n_1+n_2-.2)} = (n_1 + n_2 - 2)\frac{\mathrm{SSE}_{\mathrm{pooled}} - (\mathrm{SSE}_1 + \mathrm{SSE}_2)}{\mathrm{SSE}_1 + \mathrm{SSE}_2}$$

Because individual results appear as both dependent and explanatory variables, the estimates of the regression coefficients will be biased to some extent, and the above F-test should probably be regarded as a rough index of the difference between treatments rather than a precise probabilistic statement (cf. Pielou 1974).

To evaluate the effects of grooming on pollen carryover, the pairs of consecutive flowers were separated into three subsets depending on whether the bee walked between the two flowers, flew quickly between them in a manner resembling typical behaviour in the field, or made a long flight (or a long pause) with obviously thorough grooming recorded on the tape for the run. In transitions of the middle category, quick grooming usually did occur but it was not prolonged enough to warrant comment.

RESULTS*

Nectar effects: Erythronium americanum

Handling time

The amount of time that a bee spends on a flower increases significantly with the nectar concentration (Kruskal–Wallis test, $H = 13$, $P < 0{\cdot}001$). Substantial increases in concentration (Fig. 1a) or in volume (Fig. 1b) result in longer visits. There is a significant treatment effect of volume at both concentrations: for 12·5% nectar; $H = 9{\cdot}1$, $P < 0{\cdot}025$; for 25% nectar, $H = 26{\cdot}8$, $P < 0{\cdot}001$. However, there is no significant difference in the times spent on flowers with dispersed nectar as opposed to spatially localized nectar (Table 1).

Pollen deposition

A positive correlation is expected between the time spent on a flower and the number of grains deposited on its stigma and one would, therefore, expect that nectar-rich flowers

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* The unprocessed results of all these experiments are available and will be supplied by the author.

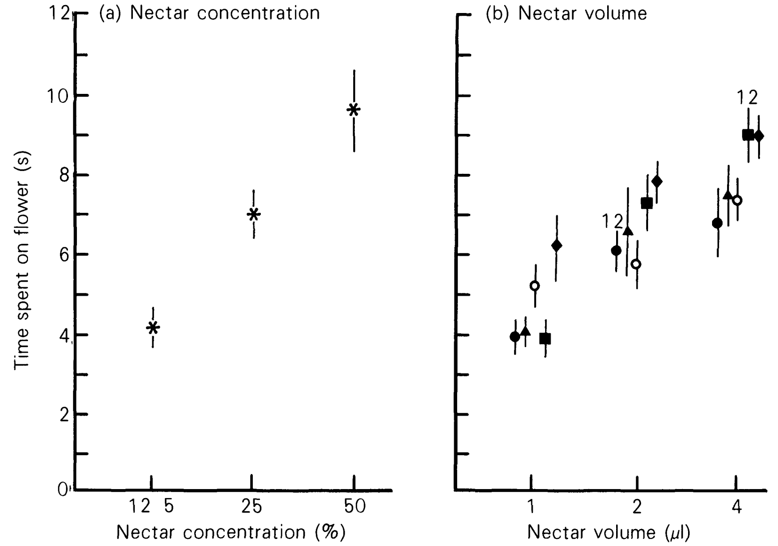

FIG. 1. Handling times of ***Bombus ternarius*** queen ('Blue') on ***Erythronium americanum*** flowers as a function of nectar (a) concentration and (b) volume. $n = 36$ for each treatment in (a); $n = 13$ in (b) except for the two points marked with a '12'. Bars are ±1 S.E. Symbols: (♦, ●), 12·5% sucrose; (■, ▲, ○), 25% sucrose; different symbols within each concentration category represent different sessions, each of which may include more than one run.

would receive more grains (Thomson & Plowright 1980). However, such a relationship cannot be detected simply, because both deposition and its variance decrease drastically as pollen is exhausted from the bee. The technique adopted here incorporates some compromises in statistical power necessitated by the structure of the data and, in general, large sample sizes would be needed to show significant effects. No relationship can be seen between nectar concentration and pollen deposition in the small sample from type-1 runs (Table 2). However, nectar volume does affect deposition (Table 3). The apparently greater deposition on nectar-rich flowers is expected from the handling times, and confirms a similar finding for bumble-bee pollination of *Diervilla lonicera* (Thomson & Plowright

TABLE 2. Analysis of the effect of nectar concentration on pollen deposition in *Erythronium americanum*

	Sucrose concentration (%)		
	12·5	25	50
Deposition greater than predicted by regression	5	5	2
Deposition less than predicted by regression	8	8	8

Table 3. Analysis of the effect of nectar volume on pollen deposition in *Erythronium americanum*

	Nectar volume (μl)		
	1	2	4
Deposition greater than predicted by regression	9	13	20
Deposition less than predicted by regression	23	20	16

1980). There are too few usable results from the type-4 runs to determine whether there is any relationship between pollen deposition and nectar dispersion within a flower; no such relationship would be expected if there were no difference in handling time.

Comparison of bee species. Erythronium grandiflorum

In three runs with two typically sized *Bombus bifarius* queens on *Erythronium grandiflorum*, it became apparent that these bees were too small to be highly efficient pollinators, at least when feeding on nectar. As a queen probed the nectaries at the base of the ovary, the tip of her abdomen usually fell short of the stigmatic surface. Although some grains were placed on the stigma, usually during the bee's arrival or departure, considerably more were deposited on the non-receptive shaft of the style. Stigmatic deposition exceeded stylar deposition on only one of nineteen flowers (5·3%). After this discovery, only the larger *Bombus occidentalis* was used, and the Colorado data reported here come from repeated runs by a single queen. The stigmatic deposits of this bee exceeded stylar deposits in 54% of the flowers. The difference between the bee species (in whether stigmatic loads exceeded stylar loads) is highly significant by a 2 × 2 contingency table ($\chi^2 = 8{\cdot}1, P < 0{\cdot}01$).

Pollen carryover

To provide a visual summary of the general patterns of carryover, the mean pollen depositions for *Erythronium americanum*, *E. grandiflorum* with dehisced or undehisced anthers and *Linaria vulgaris* are given in semi-logarithmic plots (Fig. 2a–d). Although these mean values for all runs fall into fairly straight lines, suggesting approximately exponential decay, there is noteworthy variation, as shown by the broad ranges and standard deviations.

Effects of anther dehiscence and grooming

The results from the Colorado *Erythronium grandiflorum–Bombus occidentalis* runs were tabulated and all usable successive pairs were broken down into cross-classified categories depending on: (i) whether they came from runs with dehiscent or indehiscent recipient flowers; and (ii) whether the voice tapes indicated a walk, a short flight, or a conspicuous grooming pause between the flowers of the pair. The decay exponents were used to generate the simulated carryover curves in Fig. 3. Unfortunately, conspicuous grooming pauses were comparatively rare, so sample sizes are small, especially for grooming transitions. For both dehisced and undehisced recipient flowers, the decay exponents fit the same reasonable progression: walking with no grooming allows the longest carryover; normal, brief flights, which typically include some grooming, cause faster loss of grains; and obvious grooming pauses give the fastest decay. Interestingly, the effects of grooming are apparently more marked in undehisced runs; 'walking' transitions yield a decay that is significantly slower than in 'short flight' ($P < 0{\cdot}025$) or 'grooming pause' ($P < 0{\cdot}01$) transitions. The differences between transition types on dehisced flowers are not significant in this analysis.

In all cases, the decline in deposition through a run is rapid, with much of the pollen going to the first three or four flowers (Fig. 3). There is noteworthy variation between runs in the overall amount of pollen, which probably reflects differences in the initial load of red pollen picked up by the bee.

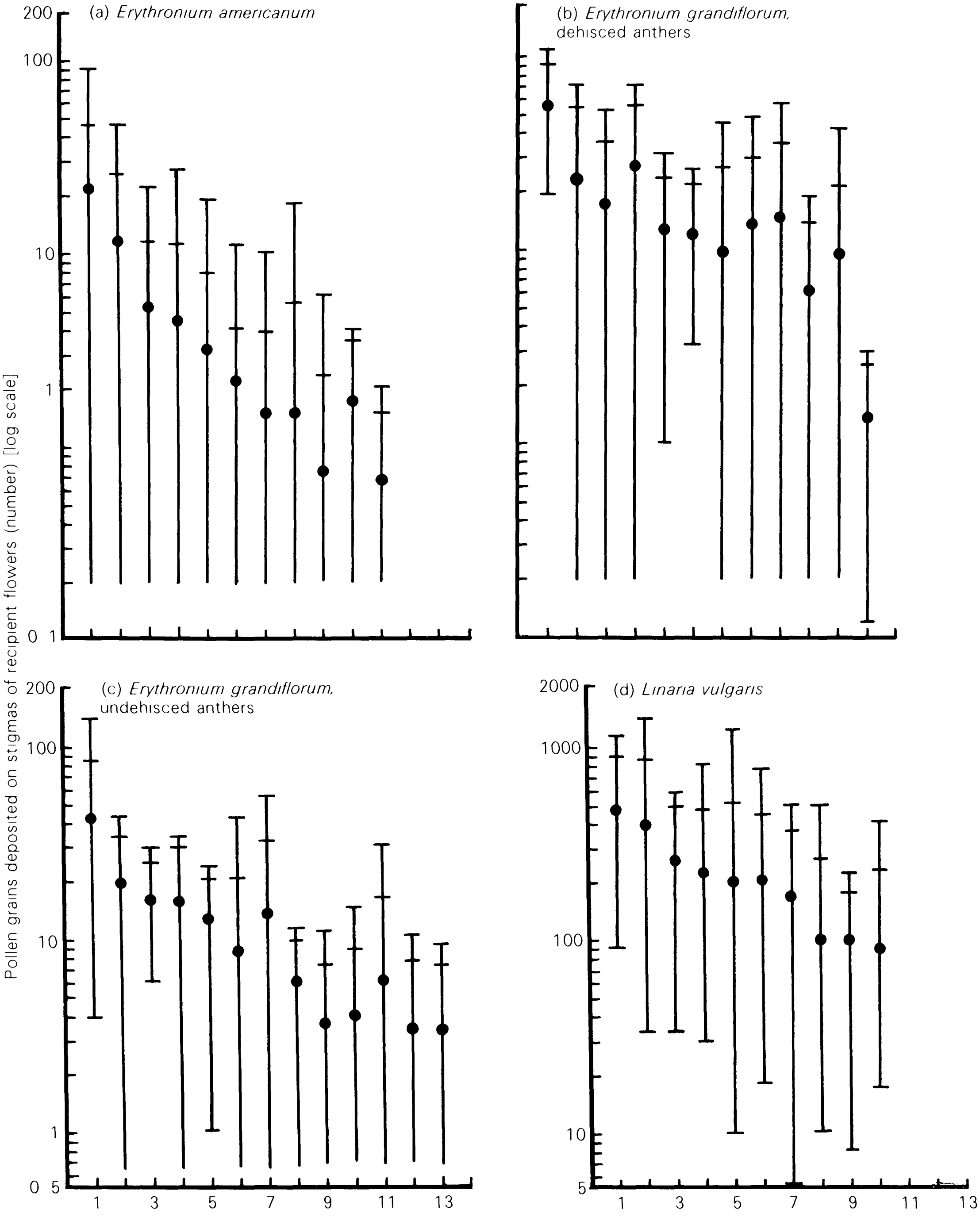

Fig. 2. Pollen deposition patterns. The (●) mean numbers of grains deposited at each recipient flower position for all the runs within a category, the maximum and minimum values observed, and (above the mean only) 1 S.D. are shown. A minimum value of zero is indicated by the lack of a terminal cross bar. (a) All runs from ***Erythronium americanum***; (b) all runs from ***E. grandiflorum*** in which anthers of recipient flowers were undehisced; (c) all runs from ***E. grandiflorum*** in which anthers were dehisced; (d) all runs from ***Linaria vulgaris***; note the different vertical scale.

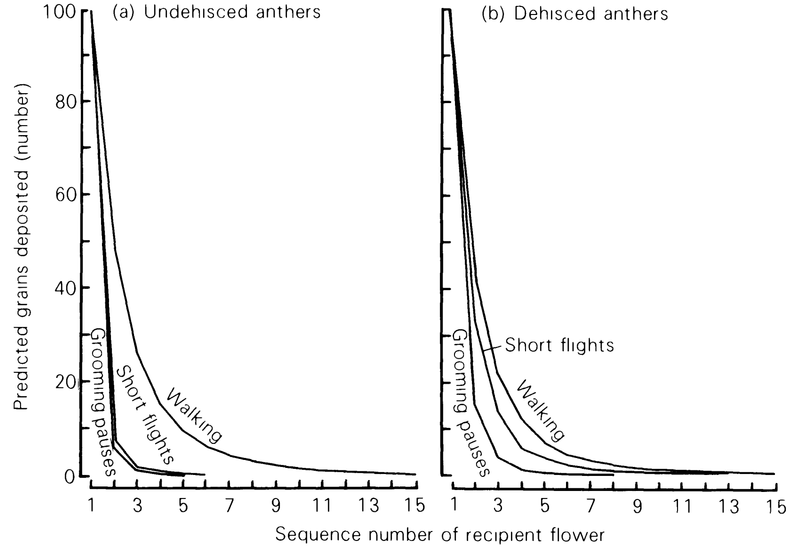

FIG. 3. Predicted pollen carryover curves for the three types of flower-to-flower transitions (walking, short flights and grooming pauses) observed in the pollination of (a) undehisced and (b) dehisced flowers of ***Erythronium grandiflorum*** by ***Bombus occidentalis***. All runs start with an arbitrary number of 100 pollen grains on the first recipient flower.

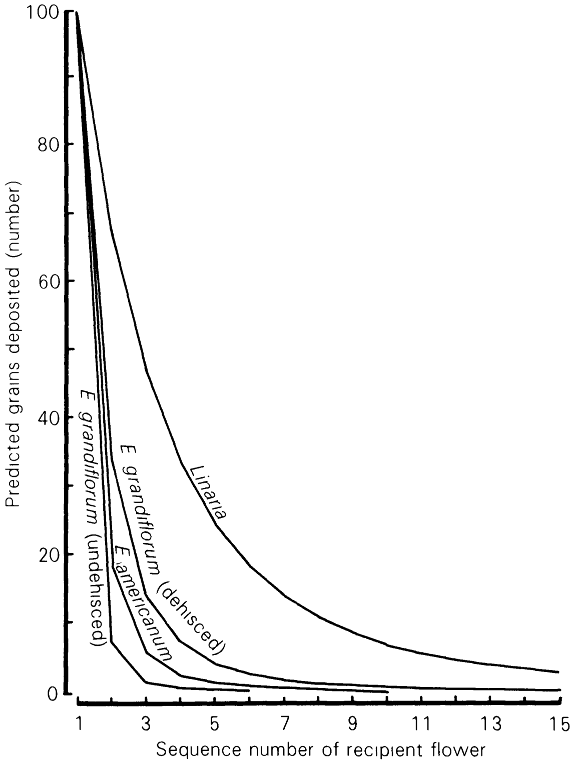

FIG. 4. Predicted pollen carryover curves for various species and states of anther dehiscence of ***Erythronium grandiflorum*** (with dehisced and undehisced anthers), ***E. americanum*** (mixed anthers) and an estimate for ***Linaria vulgaris*** (emasculated).

Comparisons among plant species

Erythronium americanum has a decay exponent (*b*) of 0·64. This figure is based on all usable data from one set of 1979 studies (Thomson & Plowright 1980) which used mostly undehisced recipient flowers, and from the 1980 results of the present study, which used mainly dehisced flowers. It is reassuring to note that the resulting carryover estimate for the mixed *E. americanum* trials falls neatly between the 'dehisced' and ' undehisced' estimates for *E. grandiflorum* ($b = 0{\cdot}77$ and $b = 0{\cdot}46$, respectively; Fig. 4). These estimates for *E. grandiflorum* omit walking transitions and those few grooming pauses that did not involve flight; thus they incorporate only 'normal' foraging, in an attempt to make them comparable to the 1979 and 1980 *E. americanum* data.

By comparison, the decay of *Linara vulgaris* pollen, in trials with emasculated recipient flowers, is drastically slower ($b = 0{\cdot}92$) than that of *Erythronium* (Fig. 4).

DISCUSSION

Nectar variation and pollination

Variation in flower-handling time by bumble bees with variation in nectar has been reported by Hodges & Wolf (1981), but see also Thomson & Plowright (1980), although Inouye (1980) and Morse (1978, 1982) have considered the nectar-extraction time to be negligible. Morse (1982) makes the reasonable suggestion that extraction time may indeed be negligible when nectar volumes are minute, as in many composite florets. Harder (1982, 1983) provides further experimental and theoretical details confirming a positive relationship between nectar and handling time when nectar volumes are more substantial. The relatively large nectar volumes in this study had a very strong effect on the time spent at a flower by *Bombus ternarius* queens. Increased concentrations had similar effects. The increases in handling times occasioned by high volumes or concentrations have two potential components. First, it may take longer for the bee to imbibe the extra volume or to extract the more viscous, higher concentration. Secondly, the higher reward levels may induce motivational changes in the bees that cause them to stay longer at rich flowers even beyond the extra time needed for extraction. Obviously, it is hard to distinguish these two components in practice, although studies of the tongue-lapping rate of bees at artificial flowers suggests that the mechanical component is the more important (J. D. Thomson & J. Grieshaber-Otto, unpublished). An analogous behavioural component has, however, been shown to increase the residence times of pollinators on multiflowered inflorescences; both bumble bees (Heinrich 1979a; Thomson, Maddison & Plowright 1982) and sunbirds (Gill & Wolf 1977) visit more flowers per inflorescence when nectar volumes are higher.

Given the highly stochastic, hit-or-miss nature of pollen deposition in *Erythronium* and similar flowers, Thomson & Plowright (1980) argued that bees which stayed longer at flowers would deposit relatively more grains, simply due to the increased chance that the stigma would touch a polleniferous area of the bee's body. This leads to the prediction that especially rewarding flowers should receive more pollen grains than expected from their position in a visit sequence. The present results confirm this for nectar volume effects. However, no significant effect of concentration was found (in a smaller data set). One would expect that more thorough studies would indeed show an effect of concentration, since the presumed mechanism—longer time spent at the flower—should apply to concentration as well as to volume. One might also expect that passive pollen acquisition by nectar-foraging bees would be higher at richer flowers, although this is much harder to show experimentally.

Perhaps the major significance of these findings is the confirmation that increased nectar secretion can be of selective advantage to an individual plant in circumstances where increased pollen deposition or acquisition increases fitness. As Thomson & Plowright (1980) argue, discussions about the evolution of 'cheating' in plants (i.e. reduced nectar rewards) should recognize that visit quality may be an important variable in addition to visit quantity (compare, for example, Heinrich 1976b).

The 'nectar dispersion' experiments (Table 1) were prompted by the hypothesis that bees which moved around more on flowers should deposit more grains than those which adopted a single feeding posture. These trials were complicated by the death of the bee ('Blue') which supplied the bulk of the data in the other trials. It was not evident that dispersing the nectar reward had the expected effect of causing more movement. Therefore, although the results are presented to show the noteworthy differences between bees, they have little to say about the effects of postural variation on grain deposition. Direct analysis of films or videotapes would be a better way to evaluate such effects.

Estimating carryover parameters

Because there have been few studies of pollen carryover, little has been said about statistical problems involved in comparing treatments. Price & Waser (1982) and Waser & Price (1982) suggest a procedure that combines data from several runs by (i) dividing each stigmatic load within each run by the maximum value for that run, and (ii) examining the regression of the resulting transformed variates on flower sequence number. There are some indications, however, that this procedure may be suboptimal for the data at hand.

Erythronium-pollen deposition curves often decay quickly to a relatively long distributional tail (Thomson & Plowright 1980). Because runs are heterogeneous, two flowers may have the same sequence numbers in different runs but have very different opportunities for pollen deposition. In cases where the bee starts a run with very little pollen it is as if the entire run consists of 'tail' (ones, twos and zeros dominate from the beginning). Such data are not well suited to the requirements of linear regression. When such a run has been transformed and pooled with others, following the Price–Waser procedure, it inevitably contributes large residuals to the overall regression which in turn widens the confidence limits on the regression parameters. True differences between treatments could be blurred by this effect.

The Price–Waser procedure also lacks the flexibility to extract certain chosen types of transitions from a run—e.g. walking *v.* flying. The 'successive pairs' analysis described above allows data to be broken down in this manner and, therefore, makes possible different experimental designs that do not impose an experimental treatment on an entire run. However, it is likely that still better methods can be found and further research is desirable. Regardless of statistical refinements, the great variability in pollen deposition guarantees that experimenters must reconcile themselves to very large sample sizes. This is especially true if one is concerned with describing the attenuated tail of the distribution, rather than simply documenting the travel of the 'average' grain.

Grooming and pollen carryover

Unlike many other pollinators, female bees actively collect pollen by grooming it from their bodies with a variety of specialized structures. Simply watching a pollen-dusted bee clean itself is enough to convince one that grooming should have a critically important role in determining the expected 'survivorship' of a cohort of grains after they are added to the active pool of pollen on a bee's body. Nevertheless, it is not easy to demonstrate the importance of grooming quantitatively, and the comparisons of Fig. 3 seem to be the first experimental evidence that there is a measurable effect.

One might expect that pollen carriage would be more extensive in animals that do not groom between flowers. This seems to be true of the hummingbird-*Ipomopsis* results presented by Price & Waser (1982); N. Waser (pers. comm.) reports that the birds did not groom during the runs, and carryover appears extensive in comparison to *Erythronium.* Lertzman's models (Lertzman, 1981; Lertzman & Gass 1983) of pollen carriage are based on hummingbird systems and also do not incorporate grooming. Realistic models for bees should include grooming losses.

The loss of *Linaria vulgaris* pollen from a bee's body seems to be much slower than that of *Erythronium* (Fig. 2), even given that the experiments are not exact parallels. This difference is most likely a grooming difference having several possible causes: first, *Linaria* grains are smaller and apparently more sticky; secondly, the specific nototribic placement of *Linaria* grains may render removal more difficult; and thirdly, the specific placement may 'bother' the bee less and therefore stimulate less grooming activity. While these causes cannot be separated at present, a peculiar observation suggests the relative importance of the first two causes. Some bees that visit *Linaria* bear seemingly permanent dorsal accretions of pollen, as if pollen has been applied faster than it can be removed. These bees scrape at the accretion with their forelegs without dislodging it. When one of these bees is used in a pollen carryover run, there is essentially no exhaustion of grains. (Such bees were not counted in the results presented above.) It seems likely that pollen is layered in these accretions, with the oldest at the bottom, and the eventual emergence and deposition of grains from the bottom layers could contribute to some very long-distance transport. Lertzman & Gass (1983) also treat layering and Thomson (1983) speculates on the antagonistic relationship between layering and grooming in bee pollination.

The concentration and volume of floral nectar are both positively related to the time a bumble bee spends at an *Erythronium* flower. Greater nectar volumes result in greater pollen deposition and a similar effect for concentration could probably be demonstrated.

Experiments confirm the reasonable suspicion that the degree of grooming by pollinators can influence the extent of pollen transport. Furthermore, the extent of transport by bumble bees can differ markedly between different plant species and the examples examined here suggest that grooming differences may be an important cause. When a plant population is served by different pollinator species (e.g. grooming bees and non-grooming birds) the pollinators may provide qualitatively different gene-dispersal services, even beyond differences in flight distances (Schmitt 1980) or 'pollination effectiveness' as usually measured (Primack & Silander 1975).

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