

Behavioral responses by bumble bees to variation in pollen availability

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Summary. Pollen-collecting bumble bees (*Bombus* spp.) detect differences between individual flowers in pollen availability and alter their behavior to capitalize on rewarding flowers. Specific responses by bees to increased pollen availability included: longer visits to flowers; visits to more flowers within an inflorescence, including an increased frequency of revisits; an increased likelihood of grooming while the bee flew between flowers within the inflorescence; and more protracted inter-flower flights, probably because of longer grooming bouts. The particular suite of responses that a bee adopted depended on the pollen-dispensing mechanism of the plant species involved. Bees buzzed previously-unvisited *Dodecatheon* flowers longer than empty flowers. In contrast, pollen availability did not significantly affect the duration of visits to *Lupinus* flowers, which control the amount of pollen that can be removed during a single visit. Simulation results indicate that the observed movement patterns of bumble bees on *Lupinus* inflorescences would return the most pollen per unit of expended energy. The increased foraging efficiency resulting from facultative responses by bees to variation in pollen availability, especially changes in the frequency and intensity of grooming, could correspondingly decrease pollen dispersal between plants.

Key words: *Bombus* – Grooming behavior – Pollen collection – Pollen dispersal

The efficiency of pollen foraging by bees simultaneously and antagonistically affects the foragers' reproductive output (or that of their colonies) and the reproductive success of the plants they visit. This efficiency will partly depend on the ability of bees to detect variation between flowers in pollen availability and to respond in a manner that enhances foraging returns. Pollen is the primary protein source for bees and is necessary for egg production by reproductive females and growth by developing

larvae (for bumble bee examples see Plowright and Pendrel 1977; Sutcliffe and Plowright 1988). Therefore, evolutionary improvements in the behavioral flexibility of bees to variation in pollen abundance should have additionally promoted reproductive output. However, such improvements should have coincidentally favored floral characters that either hinder the assessment of pollen availability by bees, or frustrate their attempts to respond to that variation.

All nonparasitic bees, except hylaeine and euryglosine colletids, collect pollen externally (Michener et al. 1978). After visiting a flower, a pollen-collecting bee grooms the pollen from its body and places it in specialized carrying structures (scopae or corbiculae), often located on its hind legs, where it is carried back to the bee's nest. Bees typically groom while flying between flowers, although they also occasionally groom while sitting on or hanging from a flower (Michener et al. 1978). Honey bees (*Apis mellifera*), and presumably other bees, have sensilla on their corbiculae which monitor the size of the growing pollen load (Ford et al. 1981).

In contrast to the expectation that bees should be able to monitor their pollen collection and respond to variation in pollen availability, Hodges and Miller (1981) and Haynes and Mesler (1984) concluded that bumble bees (*Bombus* spp.) could not determine their foraging success at individual flowers. Hodges and Miller found that bees visited few of the flowers in *Aquilegia caerulea* (Ranunculaceae) inflorescences, few of the plants in the stand, and they turned frequently as they moved through the stand. They suggested that this foraging behavior was inefficient because the frequent turning would increase the likelihood of revisiting a flower and only a small proportion of the available flowers were visited. Haynes and Mesler also observed that bumble bees visited a small number of the flowers in *Lupinus polyphyllus* (Leguminosae) inflorescences. These bees additionally began an inflorescence visit on lower flowers, which had been partially depleted of pollen, rather than on younger upper flowers, which contained abundant pollen. Pollen is hidden within a lupine flower, so that visual assess-

ment of pollen availability is unlikely. Like Hodges and Miller (1981), Haynes and Mesler (1984) concluded that bees are constrained from maximizing their foraging efficiency while collecting pollen by "... the limitations of their perceptions, behavior, and learning ability" (pg. 252).

Within this context, I initiated a study of the behavior of pollen-collecting bumble bees to determine whether they assess the amount of pollen that they remove from individual flowers and subsequently change their behavior to increase their foraging efficiency. This study specifically addressed four predictions: 1) bees should visit flowers with abundant pollen longer than depleted flowers; 2) while flying between flowers, bees should groom more frequently and more intensely after visiting a rewarding flower; 3) bees should visit more flowers in inflorescences with particularly productive flowers; and 4) bees should be more likely to visit neighboring plants after collecting pollen from a very productive plant. All of these predictions assume that bees monitor their pollen-collecting success during each flower visit and that their behavioral repertoire is not constrained by their perceptual or learning capabilities. The latter two predictions further assume an aggregated distribution of pollen between flowers within an inflorescence and between neighboring plants in a stand. Because it is unclear whether grooming is a facultative behavior, I also asked whether grooming is context-specific, or do bees always groom while flying? In addition to addressing the outlined predictions, I will consider the pollination consequences of the observed behavior, and propose explanations for the behavior observed by Hodges and Miller (1981) and Haynes and Mesler (1984).

The two plant species that are the primary subjects of this study, *Lupinus sericeus* Pursh and *Dodecatheon conjugens* Greene, were selected for three reasons. First, neither plant species produces nectar, so that the observed behavior only involved responses to variation in pollen availability. Second, the flowers of both species hide pollen from view, so that bees could only assess pollen availability by manipulating flowers. Finally, these plants use different mechanisms to dispense pollen (see Materials and methods), which necessitate different pollen-collecting techniques by bees. Similar behavior by bees visiting these plant species would therefore demonstrate the generality of their responses to variation in pollen availability.

Three recent papers addressed two of the predictions that I consider in this paper. Cane and Payne (1988) and Buchmann and Cane (1989) studied plants with poricidal anthers which require that a bee grasp the anthers with its mandibles and rapidly vibrate (buzz) its wing muscles to remove pollen. They found that bees, including bumble bees, buzzed highly rewarding, previously unvisited flowers significantly longer than visited flowers (prediction 1). Gori (1989) reported that bumble bees visited fewer flowers per visit to *Lupinus argenteus* inflorescences after he had experimentally emptied the flowers of pollen (prediction 3). As will be evident, the results presented here are consistent with these conclusions.

Materials and methods

Grooming behavior

All grooming behavior was videotaped with a Panasonic® AG-2400 portable recorder and a Panasonic® WV-D5000 camera equipped with a 12× zoom lens. This camera records an image for only 1/1000 s during every 1/60 s, thereby reducing image blurring during playback at slow speeds. Recorded behavior was analyzed at 1/7 of recorded speed.

To determine whether bees obligately groom during all flights between flowers regardless of pollen availability, naive workers from a captive colony of *Bombus occidentalis* Greene were trained to gather nectar from artificial flowers. These flowers (18×18×12 mm plexiglas cubes with a 3 mm deep well in the upper surface) were arrayed in a grid with 20 cm spacings. Each flower contained 1 µl of 30% sucrose solution (mass solute/mass of solution), but no pollen. The bees were video-taped as they visited these flowers and the video-tape was later analyzed for the frequency of grooming.

An additional experiment examined whether the likelihood of grooming depended on opportunity, as influenced by the distance between flowers. This experiment was part of a larger study of dispersal of *Aconitum delphinifolium* DC pollen by *Bombus flavifrons* Cresson and *B. mixtus* Cresson workers. *Aconitum* flowers are strongly protandrous, with a 5-day male phase and a 3-day female phase during which no pollen is available. A sequence of inflorescences, spaced 30 cm apart, was arranged in a screen flight cage (3.7×3.7×2.1 m). The sequence began with a female-phase inflorescence followed by a single-flowered male-phase inflorescence and a series of inflorescences with one to four female-phase flowers. Female-phase flowers had been emasculated before anther dehiscence, so that they never contained free pollen. Bees were captured as they fed on *Aconitum* and placed in a small box until they became languid when one bee was placed on the first female-phase inflorescence. During an acceptable trial the bee drank nectar and warmed up on the initial inflorescence, visited the male-phase flower and then at least 10 female-phase flowers. Each trial was video-taped and the frequency of grooming during flights between inflorescences was compared with the frequency between flowers within inflorescences.

A weighted, repeated-measures analysis of variance was conducted to assess whether the likelihood of grooming differed during flights between inflorescences, or between flowers within an inflorescence. This analysis used logit transformations of the proportion (p_g) of all flights between or within inflorescences that involved grooming ($\log\text{odds} = \ln[p_g/(1-p_g)]$; Neter et al. 1985). Each observation was weighted by the inverse of the variance for a logit based on n observations ($n p_g[1-p_g]$) to adjust for the dependence of the variance of a logit on the mean.

Behavior on *Dodecatheon*

Dodecatheon conjugens produces a few-flowered inflorescence on a leafless scape; seldom do more than two flowers bloom simultaneously. *Dodecatheon* flowers have an exposed cone of introrse anthers which dehisce gradually from the tip to the base over at least two days. While visiting a *Dodecatheon* flower a bumble bee grasps the anther cone with its mandibles, curls its body beneath the anthers, and then buzzes pollen from the flower (see Macior 1964).

The *Dodecatheon* experiments addressed two specific questions: do bumble bees buzz previously-unvisited flowers longer than depleted flowers; and is a bee more likely to visit an adjacent flower after visiting a flower with abundant pollen (area-restricted search). Single-flowered inflorescences in a dense stand of *D. conjugens* at Sibbald Flat, Alberta (51°02'N; 114°49'W) were covered with fine-mesh bags before anthesis to exclude insects. After anthesis, pairs of flowers were picked and assigned to one of two treatments;

pollen intact, or pollen removed. For the latter treatment, pollen was removed by flicking the anther cone with a finger several times. The scape of each flower was placed in separate water-filled vials which were located 10 cm apart at the end of a forked stick. These flowers were then placed near a bumble bee queen that was freely visiting *Dodecatheon* flowers. If the bee visited the experimental flowers, I recorded the duration of the buzzes and the sequence of flower visits.

The hypothesis concerning area-restricted search assumes an aggregated dispersion of pollen within a stand of plants. To assess this assumption, all open *Dodecatheon* flowers from a 2 × 2 m plot at the Sibbald Flat study site were collected and separately preserved in 70% ethanol. The coordinates of each flower within the plot were recorded, so that inter-flower distances could be calculated. The pollen was later sonicated from the flowers with an ultrasonic cleaner and counted with a Particle Data® Elzone 180XY particle counter (see Harder 1990). The pollen counts were then analyzed to determine whether pollen availability was spatially autocorrelated (see Cliff and Ord 1981) within the plot with SAAP, a program written by D. Wartenberg (Department of Environmental and Commercial Medicine, R.W. Johnson Medical School, Piscataway, New Jersey).

Behavior on *Lupinus*

Lupinus sericeus racemes comprise several whorls that each include five or six flowers. Flowering proceeds up the inflorescence with 10–20 flowers in bloom at one time. Lupine flowers resemble those of other papilionaceous legumes in that the stamens and pistil are hidden between the keel petals. However, unlike many legumes, the adjacent margins of the keel petals are fused, except at the distal apex. Lupine stamens shed their pollen before anthesis and during subsequent elongation they push the pollen into the tip of the keel petal around the hairy stigma (see Dunn 1956; Wainwright 1978; Juncosa and Webster 1989).

Video-taped records of *Bombus bifarius* Cresson workers visiting *Lupinus sericeus* illustrate that a bee depresses the wing petals, which surround the keel petals, with its metathoracic legs while bracing itself against the banner petal with its head and mesothoracic legs. This action forces the stigma through the pollen and out of the aperture at the tip of the keel petals. The bee removes this pollen with its prothoracic legs (raking). After the bee leaves the flower, the stigma returns to its original position within the keel, so that subsequent visits repeat the action of the stigmatic pollen-dispensing mechanism. Unlike many *Lupinus* species (see Wainwright 1978; Gori 1989), *L. sericeus* flowers do not change color after being pollinated.

To examine the behavioral responses of bees collecting pollen from *L. sericeus* flowers, free-foraging *Bombus bifarius* workers were video-taped near Stimson Creek, Alberta (50°17'N; 115°12'W). Each bee was observed visiting only a single inflorescence. Some of the inflorescences had been previously bagged, so that none of their open flowers had been previously visited (unvisited inflorescences). The remaining inflorescences were left exposed to the normal frequency of bee visits (visited inflorescences). For each bee, I recorded: the number of open flowers in the inflorescence; the number of visits each flower received; the duration of each visit; the duration of each flight between flowers in an inflorescence; and whether the bee groomed as it flew between flowers. To quantify the pattern of pollen availability within an inflorescence, one flower of each whorl from 20 unbagged inflorescences was collected, preserved and the pollen counted as described above.

Results

Grooming behavior

Six *Bombus occidentalis* workers were trained to visit artificial flowers for nectar. These bees seldom groomed

while flying between flowers. In total, three bees groomed during six of the 341 flights recorded for all bees.

In contrast, the 11 *B. flavifrons* and *B. mixtus* workers observed on *Aconitum* groomed much more frequently, even though most of the flowers visited were in female phase and therefore contained no pollen. Bees groomed proportionately more often when flying between inflorescences (mean $p_g = 0.85$, lower SE = 0.799, upper SE = 0.886) than when flying between flowers within an inflorescence (mean $p_g = 0.33$, lower SE = 0.264, upper SE = 0.398: repeated-measures ANOVA, $F_{1,10} = 28.72$, $p < 0.001$). Ten of the 11 bees groomed immediately after visiting a male-phase flower.

Behavior on *Dodecatheon*

Bombus bifarius and *B. melanopygus* Nylander queens apparently monitored their pollen-removal success during flower visits to *Dodecatheon conjugens*, as they buzzed unmanipulated flowers significantly longer (mean = 1.8 s, lower SE = 1.63 s, upper SE = 1.93, $n = 32$) than depleted flowers (mean = 1.0 s, lower SE = 0.95 s, upper SE = 1.10 s, $n = 30$: two-factor ANOVA, $F_{1,58} = 18.05$, $p < 0.001$, based on log-transformed data). The species differed in buzz durations, with the smaller *B. bifarius* buzzing longer (mean = 1.5 s, lower SE = 1.37 s, upper SE = 1.59 s, $n = 45$) than *B. melanopygus* (mean = 1.0 s, lower SE = 0.92 s, upper SE = 1.13 s, $n = 17$: $F_{1,58} = 9.90$, $p < 0.005$); however, the two species did not respond differently to the presence of pollen (interaction, $F_{1,58} = 1.23$, $p > 0.25$).

The likelihood that these bees would visit the second experimental flower of each pair did not depend on the state of the first flower visited (73% rejection rate after visiting one of 26 empty flowers; 47% rejection rate for 17 full flowers: $G = 2.97$, $p > 0.05$). This lack of response could result either because the bees did not forage in a manner that maximized pollen collection, or because finding abundant pollen in one flower normally provided little information about pollen availability in adjacent flowers. The latter explanation seems more likely as pollen availability varied independently among 61 neighboring *D. conjugens* plants in a 2 × 2 m plot (spatial autocorrelation, Moran's $I = 0.017$, $SD = 0.219$, $E(I) = -0.017$, $p > 0.1$).

Behavior on *Lupinus*

The standing crop of pollen in *Lupinus sericeus* flowers declined progressively from the top whorl down (Fig. 1), because the older lower flowers had received more bee visits. An exponential function ($Y = \exp[10.162 - 0.389X]$) describes this relation satisfactorily ($F_{1,76} = 136.07$, $p < 0.001$, $r^2 = 0.727$, analysis of covariance comparing 20 plants) and indicates that flowers in a given whorl contained 32.2% less pollen, on average, than flowers in the whorl immediately above. Individual plants differed in pollen availability (analysis of covari-

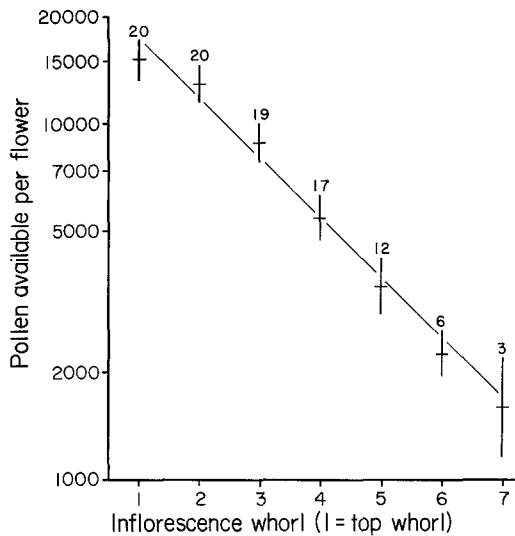


Fig. 1. Relation between the standing crop of pollen in *Lupinus sericeus* flowers and their position within an inflorescence relative to the uppermost open flower. Each bar represents the mean (\pm SE) pollen availability for the number of flowers indicated

ance, $F_{19,76} = 2.26$, $p < 0.01$); however, standing crop of pollen declined similarly within inflorescences for all plants (test for homogeneous slopes, $F_{19,57} = 1.34$, $p > 0.1$).

The behavior of *Bombus bifarius* workers changed dramatically when they encountered an unvisited lupine inflorescence. On visited inflorescences the median bee visited 5 flowers without any revisits, took 0.6 s to fly between flowers, and groomed during 81% of the 159

Table 1. Comparisons of the behavior of *Bombus bifarius* workers collecting pollen on previously-visited ($n = 28$) and previously-unvisited ($n = 29$) *Lupinus sericeus* inflorescences. The median (\pm one quartile) response is presented in all cases, except for the proportion of interflower flights associated with grooming (mean \pm SE)

	Previously visited	Not previously visited	Test statistic	p
Number of flowers available	11 8.5–15	12 11–14	0.68 ^a	> 0.25
Total number of flower visits	5 3–9.5	33 13–56	25.36 ^a	< 0.001
Number of visits per flower	1 1–2	3 2–5	17.57 ^b	< 0.001
Visit duration (s)	0.6 0.53–0.70	0.7 0.61–0.80	2.70 ^b	> 0.1
Duration of interflower flights (s)	0.6 0.56–0.81	0.9 0.81–0.97	15.80 ^b	< 0.001
Proportion of interflower flights associated with grooming	0.806 0.770–0.837	0.975 0.969–0.979	58.54 ^c	< 0.001

^a Wilcoxon two-sample test, χ^2 with 1 df

^b Wilcoxon two-sample test based on medians for each bee, χ^2 with 1 df

^c Weighted nested ANOVA based on logit-transformed data, F with 1 and 55 df

flights (Table 1). In contrast, the median bee on unvisited inflorescences visited 33 flowers, with 3 visits per flower, took 0.9 s in flight and groomed during 97% of the 938 flights. These differences occurred even though visited and unvisited inflorescences included equivalent numbers of flowers (Table 1). In contrast to these responses to variation in pollen availability, the duration of flower visits did not differ between visited and unvisited inflorescences (Table 1).

Discussion

Bumble bees collecting pollen from *Dodecatheon conjugens* and *Lupinus sericeus* detected and responded to differences between flowers in pollen availability, even though both species conceal pollen from view (also see Cane and Payne 1988; Buchmann and Cane 1989; Gori 1989). These responses included: changes in the duration of flower visits (*Dodecatheon*); changes in grooming (*Lupinus*); and changes in movement patterns within inflorescences (*Lupinus*). Although some expected responses were not observed (see below), this lack of response seems to be a consequence of plant-imposed constraints, rather than behavioral limitations of the bees (see also Thomson 1988).

Bees were expected to visit flowers with abundant pollen longer than depleted flowers. This was true for *Dodecatheon*, but not for *Lupinus*, even though both experiments involved the same bee species, *Bombus bifarius*. Longer buzzes should remove more pollen from *Dodecatheon* flowers, as they do for *Pedicularis contorta* (Harder 1990), another buzz-pollinated plant with a different flower structure. In contrast, the pollen dispensing mechanism of *Lupinus* flowers probably precludes any advantage to longer flower visits. During a single visit to a lupine flower, a bee can only remove the pollen presented on the stigma, regardless of pollen availability. *Lupinus sericeus* flowers produce approximately 20000 pollen grains, of which 18.9% (median) is removed during the first visit to a flower and 5.4% is removed during the fifth visit (Harder 1990). While visiting a lupine flower, a bee spends most of its time positioning its body and depressing the wing and keel petals. Hence, although the stigma presents a decreasing number of grains with each visit, this change is probably not sufficient to result in shorter visits. Additional pollen can be removed from a *Lupinus* flower, but a bee must leave the flower to allow the keel to return to its original position. Consequently, bees on unvisited inflorescences frequently moved back and forth between two adjacent flowers before moving to other flowers in the inflorescence. The high frequency of revisits on unvisited inflorescences indicates that bees did respond to increased availability of lupine pollen. but the form of the response was constrained by the plant's dispensing mechanism.

The probability of a bumble bee grooming in flight depends on opportunity and incentive. When visiting artificial flowers without pollen, bees rarely groomed indicating that grooming is a facultative behavior. Observations of bees visiting female-phase *Aconitum* flow-

ers reveal the opportunistic nature of grooming: grooming was considerably less likely during brief flights between flowers within an inflorescence than during longer flights between inflorescences. The frequency and intensity of grooming are further affected by variation in pollen availability as the lupine experiments demonstrated (Table 1). Indeed, grooming should rightfully be considered a component of handling time for a pollen-collecting bee.

Given that bumble bees can recognize and respond to variation in pollen availability, they should locally concentrate their foraging to maximize pollen collection when they encounter an abundance of pollen. The bees visiting *Lupinus* flowers did restrict their search when they moved to an unvisited inflorescence: they visited more flowers per inflorescence and revisited flowers more often (Table 1; also see Gori 1989). In contrast, the bees visiting *Dodecatheon* were not more likely to visit a neighboring flower after visiting a productive flower. However, area-restricted search would probably not be profitable for these latter bees, because pollen availability in neighboring flowers was not significantly correlated.

The economics of pollen collection

The observed responses of bumble bees to differences in pollen availability would enhance a bee's foraging return and suggest that economic principles underlie the foraging decisions of pollen-collecting bees. Why then did Hodges and Miller (1981) and Haynes and Mesler (1984) conclude otherwise? The most likely explanation is that their expectations of what constituted economically appropriate behavior were incorrect.

Hodges and Miller (1981) studied *Aquilegia caerulea*, which has protandrous flowers with a 4–5 day male phase and presents its pollen on many exposed anthers (Miller 1978). Percival (1955) demonstrated that anthers dehisce roughly sequentially throughout the male phase in the Ranunculaceae, including a species of *Aquilegia*, thereby periodically replenishing the pollen supply within a flower. Because *A. caerulea* anthers are exposed, bumble bees could visually assess pollen availability without landing on a flower, as Zimmerman (1982a) observed for *Potentilla gracilis*. Indeed, pollen-collecting bees often select particularly productive flowers based on floral structure or flowering stage (Wainwright 1978; Galen and Plowright 1985; Wolfe and Barrett 1987; Pellmyr 1988). When pollen availability can be assessed remotely, visits to neighboring plants should only occur if abundant pollen is visible and the chance of revisiting a recently visited flower will be greatly reduced. Hence a bee that bypassed several unproductive neighboring plants and turned frequently as it moved through an *Aquilegia* stand, as Hodges and Miller observed, could collect pollen more quickly than a bee that systematically visited adjacent plants along a straight foraging route.

Haynes and Mesler (1984) concluded that bumble bees did not forage as efficiently as possible on *Lupinus polyphyllus* after observing that bees generally began in-

florescence visits on less productive middle flowers and then moved upwards to more rewarding flowers (see also Zimmerman 1982b; Galen and Plowright 1985) and that bees seldom revisited flowers, even though they contained considerable pollen. The observations presented here for previously-visited *L. sericeus* inflorescences parallel those of Haynes and Mesler in several ways: pollen availability increased in upper flowers (Fig. 1); bumble bees visited few flowers in an inflorescence and seldom revisited flowers (Table 1); and they often began a visit on lower flowers (13 visits began on the top whorl [whorl 1], 8 on whorl 2, 5 on whorl 3 and 2 on whorl 4). However, the behavior of bees on unvisited inflorescences (Table 1) indicates that they monitored their pollen returns on a flower-by-flower basis and changed their behavior when pollen was abundant (see also Gori 1989). Why then did they not consistently begin visits to inflorescences on top flowers?

To determine whether a bee's starting position within a lupine inflorescence affects its foraging return, I simulated bee visits to 1000 inflorescences. These simulations incorporated the observed between- and within-inflorescence variation in pollen standing crop (see Fig. 1 and Appendix) and some simple movement rules (see Appendix). The results indicate that the starting position that would maximize the amount of pollen collected per unit of energy expended depends on the bee's departure rule (Fig. 2). The more below-average flowers that a bee will tolerate before leaving an inflorescence, the lower it should begin its visit. Overall, the most efficient behavior would involve beginning the visit on the second highest whorl and leaving the inflorescence after visiting two substandard flowers. A bee following this policy would visit an average of 4.2 flowers per inflorescence. A policy

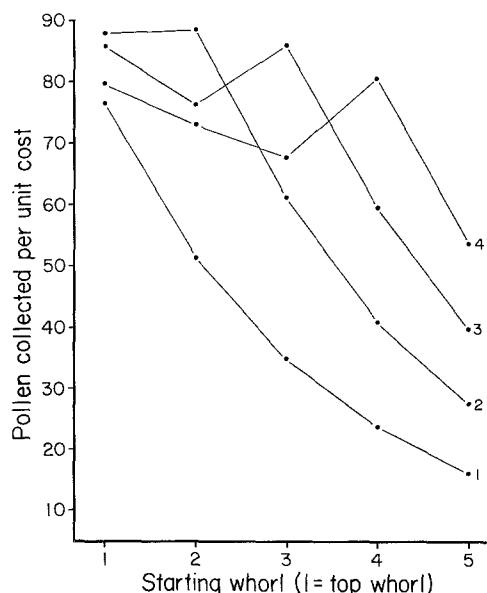


Fig. 2. Dependence of pollen-collection efficiency on a bee's starting position in a lupine inflorescence. Each point in a curve relates the mean of simulated visits to 1000 inflorescences (see Appendix: in all cases $SE \leq 1.1$). The curves depict the influence of a bee's departure rule (i.e. leave the inflorescence after visiting 1, 2, 3, or 4 below average flowers)

of starting on the third highest whorl and leaving after three substandard flowers would be almost as efficient and would result in an average of 6.3 visits per inflorescence. For these two departure rules the penalty in lost efficiency for beginning a visit higher than the optimal whorl would be small.

Bees collecting pollen from previously-visited *Lupinus sericeus* inflorescences behaved in a manner consistent with the most efficient behavior predicted by the simulation model. As mentioned above, most bees began their visits on the top two or three flower whorls. In addition, these bees visited a median of five flowers on an inflorescence before departing (Table 1). This consistency results even though the simulation model did not incorporate features specific to bees visiting lupine, other than the distribution of pollen. Bees may not employ the movement rules adopted for the model; however, if they do, their observed behavior would return the greatest amount of pollen per energetic effort. Furthermore, the observed behavior provides little indication that perceptual, behavioral or learning constraints affect pollen foraging by bumble bees.

Pollination consequences

Behavioral responses that increase a bee's pollen collection necessarily decrease the plant's pollen dispersal. Because less than 1% of the pollen leaving a flower reaches the stigmas of subsequently visited flowers (Levin and Berube 1972; Harder and Thomson 1989), this decrease in pollen dispersal could greatly restrict a plant's opportunities to function as a male. This problem is particularly acute for plants that do not produce nectar, such as *Dodecatheon* and *Lupinus*, because pollen functions jointly as the vehicle of male gametes and as the sole pollinator attractant.

Harder and Thomson (1989) observed that the proportion of pollen leaving a flower that is subsequently deposited on stigmas declined as the total number of grains removed increased. They suggested that this decelerating relation between pollen removal and dispersal could result from differential grooming responses by bees to pollen availability. Specifically, if bees groomed more often and more intensely after removing a large amount of pollen from a flower, then a smaller proportion of the removed pollen would remain on the bee's body where it could later contact a stigma (see also Thomson 1986). The bees visiting *Lupinus* responded in this manner when they encountered an unvisited inflorescence (Table 1).

This relation between pollen removal and grooming could promote at least three evolutionary responses by plants: restriction of the amount of pollen removed during individual visits through the development of packaging and dispensing mechanisms (reviewed by Harder and Thomson 1989); placement of pollen on poorly-groomed locations on the pollinator's body (Macior 1982); and production of more pollen grains to compensate for grooming losses, either by producing smaller grains (Buchmann 1983), or by increasing the allocation

of resources to pollen production (Pellmyr 1985, 1986). However, the effectiveness of the latter response in promoting pollen dispersal could be limited because increased availability promotes longer bee visits (e.g. *Dodecatheon* experiments), which result in greater pollen removal per visit (Harder 1990), and more frequent revisits (e.g. *Lupinus* experiments). Coincidental development of packaging and dispensing mechanisms, or alteration of flower morphology to place more pollen in safe sites on pollinators' bodies would alleviate this problem.

The behavior of pollen-collecting bees visiting *Dodecatheon* and *Lupinus* depended in part on the plant's pollen dispensing mechanism, which determined both the bee's pollen-collection technique (buzzing or raking) and the scope for efficient responses. Within these extrinsic constraints, bumble bees behaved in a manner that would tend to maximize the amount of pollen collected per unit of effort. Their obvious responses to abundant pollen indicate that pollen-collecting bees do monitor their foraging return from individual flowers and emphasize the costs that plants must pay when using bees as agents of pollen dispersal.

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Appendix

Simulation of pollen collection from lupine

Simulating pollen collection by a bumble bee from a *Lupinus sericeus* inflorescence required specifying: the pattern of pollen availability; the bee's movement rules; and the benefits and costs of individual visits to flowers. Empirical estimates of these parameters were incorporated whenever they were available.

Simulated inflorescences included five whorls with five flowers each. Average pollen availability (P) for a given whorl (W) was determined from a linear prediction equation ($\log[P] = a + bW$) with a randomly drawn intercept (normal distribution; mean = 10.162, variance = 0.0396) and a slope of -0.389 (see Fig. 1). The deviation of an individual flower from this mean was randomly drawn from a normal distribution with mean = 0 and variance = 0.2515.

The simulated bee began an inflorescence visit at a specified whorl. During each flower visit, it removed 10% of the available pollen. If the amount of pollen removed equaled or exceeded the average available for the respective whorl in the population as a whole, the bee moved to the next flower in the whorl. When the bee removed less than the population average, it confronted two options. If the bee had yet to encounter a threshold number of below-average flowers (departure rule), it either moved up one whorl, or down to the highest unvisited whorl if it was already visiting the top whorl. Alternatively, the bee left the inflorescence after encountering more below-average flowers than the departure rule. Because of within-whorl variation in pollen availability, a visit to an individual flower may not provide an accurate measure of the overall pollen availability in the inflorescence. Hence, leaving

an otherwise better-than-average inflorescence after visiting a single substandard flower may not result in the most efficient pollen collection. Separate simulations for different departure rules were therefore conducted to examine the importance of a bee's departure rule on the most efficient starting position. Although the relevance of the marginal-value decision rule to pollen-foraging bees has not been examined, it provides a consistent explanation for the movement patterns of nectar-collecting bumble bees (Hodges and Wolf 1980). Bumble bees also behave as though they discriminate correlations between floral characters and rewards (Harder 1988), as these movement rules require.

The energetic costs of pollen collection should depend on the relative expenditures of time and energy on flight. Bumble bees spent as much time visiting a previously-visited lupine flower as they did flying between two flowers within an inflorescence (Table 1). The average duration of a flight between inflorescences was specified to be three times greater than a within-inflorescence flight. A flying bumble bee expends approximately 10 times more energy per second than when it is at rest (Heinrich 1975). Hence, for these simulations a flower visit cost one unit of energy, a flight within an inflorescence cost 10 units for each movement between adjacent flowers or whorls (flights between more distant whorls cost proportionately more), and a flight between inflorescences cost 30 units.

Assessment of the relative benefits of different behaviors requires a measure of their utility to the bee. Nectar-collecting bees behave as though they maximize their rate of net energy uptake (Harder and Real 1987). Unfortunately, this is an inappropriate utility function for pollen-collecting bees for two reasons: pollen is collected as a primary source of protein, so that benefits (pollen collected) and costs (energy expended) involve different currencies; and pollen is collected to feed larval bees, so that adult bees realize little direct benefit from their efforts. In the absence of any observations bearing on the appropriate utility function for pollen collection, I have considered the ratio of the amount of pollen collected from an inflorescence to the accrued costs.

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