Heterogeneity Among Floral Visitors Leads to Discordance Between Removal and Deposition of Pollen

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HETEROGENEITY AMONG FLORAL VISITORS LEADS TO DISCORDANCE BETWEEN REMOVAL AND DEPOSITION OF POLLEN

Paul Wilson[1] and James D. Thomson[1]

Flowers are often visited by many species of animals. These sometimes differ in size, behavior, and other characteristics that translate into differences in their effectiveness as pollinators (e.g., Schemske and Horvitz 1984, 1988, Herrera 1987, Young 1988). The differences may be manifest in their effect on reproductive success either through female or through male function (Lloyd and Yates 1982, Bell 1985, Campbell 1989, Snow 1989). A number of recent studies have measured pollen removal as a component of male function (Snow and Roubik 1987, Cruzan et al. 1988, Galen and Stanton 1989, Harder and Thomson 1989, Thomson and Thomson 1989, Wolfe and Barrett 1989, Harder 1990, Murcia 1990, Young and Stanton 1990); however, high pollen removal need not result in high subsequent deposition of the removed pollen or in high success at siring seeds. Here we provide an example in which pollen-collecting bees remove more pollen but deposit less of it than nectar-collecting bees. The pollen collectors are antagonists with regard to the male re-

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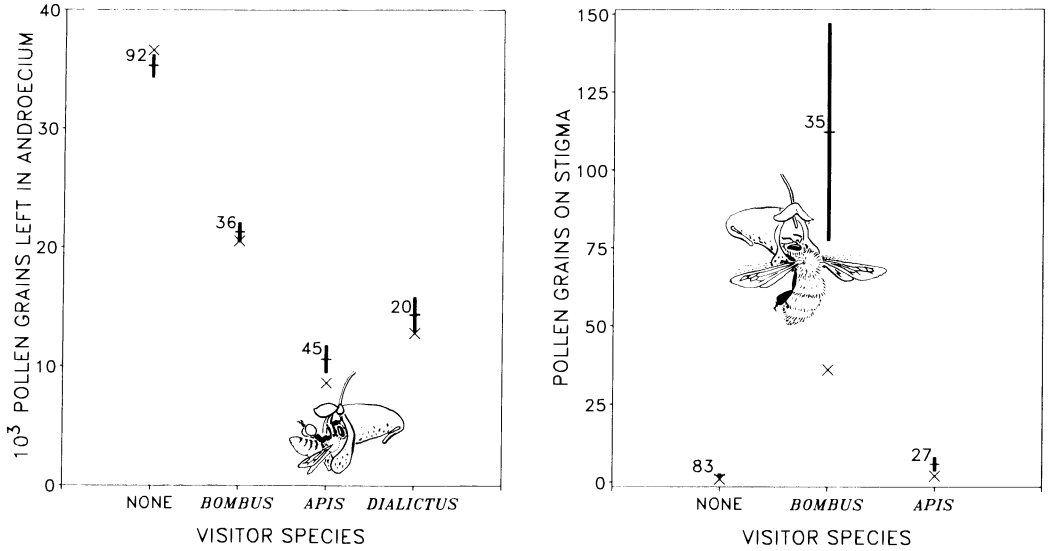

FIG. 1. The effects of single visits on pollen movement by different visitors. Unvisited flowers are denoted as "none." *Bombus* were collecting nectar as shown in right panel, *Apis* were collecting pollen as shown in left panel, and *Dialictus* were collecting pollen. Pollen collectors removed more pollen than *Bombus* and deposited less. For pollen left, there were significant ($P < .05$) differences between genera in each compared pair except *Apis* vs. *Dialictus*, which comparison was marginally significant ($P < .1$; no transformation used). For pollen deposited, there were significant ($P < .05$) differences between genera in each pair (rank transformation used). In both cases, these were least-significant-difference comparisons; a separate Type I error was risked for each comparison. Bars are means ± 1 SE; ×'s are medians; numbers are sample sizes.

productive success of the plants, at least relative to the more beneficent nectar collectors. Our results underscore the need to study pollen deposition in conjunction with pollen removal.

Materials

We studied pollen movement in *Impatiens capensis* Meerb. (jewelweed) at the Weld Preserve of the Nature Conservancy on Long Island, New York (40°53′ N, 73°12′ W). This annual plant produces many protandrous flowers. The male phase lasts 43.8 ± 1.91 h ($\bar{X}$ ± 1 SE, $N = 30$), until the androecium falls off, exposing the gynoecium, whose stigma up to that point could not have received any pollen. The female phase lasts 32.3 ± 2.29 h ($N = 31$) (cf. Schemske 1978). The gynoecium typically contains five ovules, and seed set is high. The perianth consists of two small sepals, an upturned banner-like petal, two landing-platform petals, and a large vestibular sepal that narrows into a recurved nectar spur. The androecium (in male phase) or gynoecium (in female phase) extends down from the roof of the vestibule at the front.

Here we consider two patches of flowers—Patches 1 and 2—and the visitors at those patches. *Apis mellifera* L. at these sites (though not at others) actively collected pollen, using their mouth parts to pick at the androecium while hanging upside down (see Fig. 1). *Dialictus rohweri* (Ellis) collected pollen upside down with their legs, and sometimes would subsequently crawl into the vestibule to drink nectar. *Bombus impatiens* Cresson and *Bombus vagans* Smith collected nectar, crawling into the vestibule right side up to drink from the spur, and, in the process, passively brushing the androecium or gynoecium against the backs of their thoraces (see Fig. 1). Patch 1, studied during late August 1989, had a mixed suite of visitors—mostly *Apis* and *Dialictus* with a few *Bombus*. At arbitrarily designated flowers we observed 85 visits by pollen collectors (67%) and 42 visits by nectar collectors (33%). Patch 2, studied during early September 1989, was visited almost entirely by *Bombus*, mostly *B. impatiens*. At designated flowers we observed 5 visits by pollen collectors (6%) and 78 visits by nectar collectors (94%). Overall visitation rates were similar at the two populations. Some visitors also or alternatively robbed flowers by biting into the spur to get at the nectar (Zimmerman and Cook 1985), but such visits are not germane to our results. The two patches were ≈0.5 km apart.

Methods

We labeled flowers with a small piece of tape on the pedicel and covered them with glassine envelopes. Two

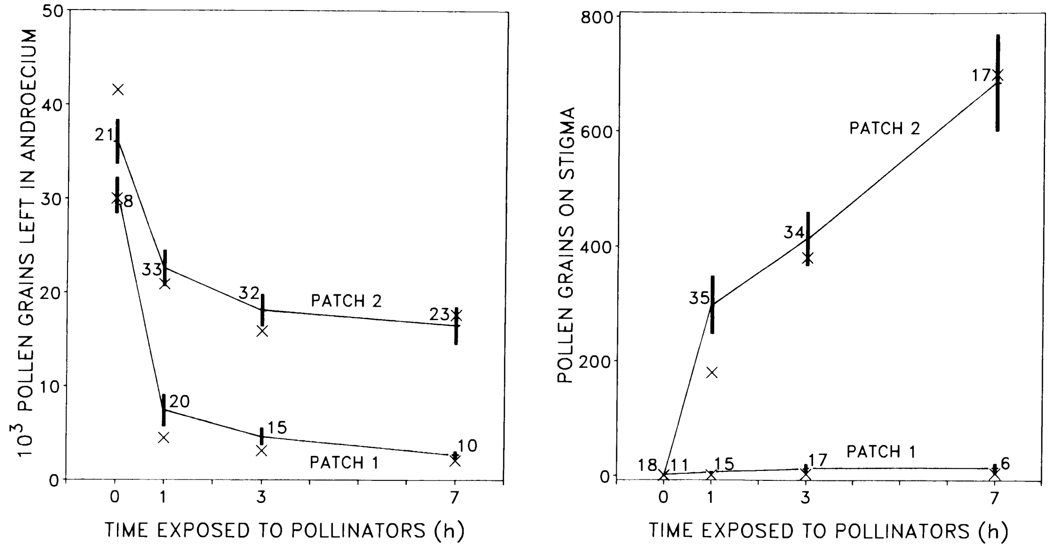

FIG. 2. The effects of suites of visitors on pollen movement in two patches (Patch 1—many pollen collectors and some *Bombus*, Patch 2—mostly *Bombus*). More pollen was removed faster in Patch 1 than in Patch 2, and much less pollen was deposited. For pollen left, there was a highly significant interaction between patch and duration-of-exposure-to-visitors ($P < .0001$; log transformation used). For pollen deposited, there was a highly significant interaction ($P < .0001$; rank transformation used). These were Model I ANOVAs. We do not imply that we have replicated the type of patch (mixed-visitors vs. *Bombus*), merely that the two patches were different. The unreplicated difference is consistent with the difference in the composition of the visitor suites and the effects of individual visits shown in Fig. 1. Bars are means ± 1 SE; ×'s are medians; numbers are sample sizes.

types of flowers were involved: buds that would open in the bags and become virgin male-phase flowers, and emasculated male-phase flowers that in the bags would become receptive virgin female-phase flowers. The next day flowers were unbagged, and animals were allowed to visit them. For one data set, a single visit was allowed to each flower and the visitor's species and behaviors were recorded. This allowed us to quantify, for different visitors, the single-visit components of pollen transfer. For a second data set, a number of flowers were exposed for a fixed interval during which there occurred an unrecorded number of visits—flowers were exposed for 0, 1, 3, or 7 h on 20 August in Patch 1 and on 9 September in Patch 2. Thus, we examined the net effects of multiple visits by different pollinator faunas.

For both studies, we measured two dependent variables: pollen not removed from the androecia of male-phase flowers, and pollen deposited on the stigmas of female-phase flowers. To measure pollen not removed, the androecium was put in a microcentrifuge tube, air-dried, preserved in 70% ethanol, later sonicated for 30 min to separate grains, diluted with 1% NaCl to 200 mL, and subsamples were counted with a Coulter electronic particle counter (Harder et al. 1985). To determine pollen deposited, we squashed the stigma in warmed glycerine jelly tinted with basic fuchsin, and later counted the grains under a compound microscope (Beattie 1971). All counts were done in random order.

Results

Single visits by nectar-collecting *Bombus* and by pollen-collecting *Apis* or *Dialictus* had significantly different consequences for pollen transfer (Fig. 1). Pollen collectors removed almost twice as much pollen as *Bombus* when visiting a virgin male-phase flower, but deposited an order of magnitude less on stigmas of virgin female-phase flowers. Moreover, *Apis* and *Dialictus* appeared to avoid female-phase flowers, in contrast to *Bombus* (also see Bell et al. 1984), so the pollen wastage by pollen collectors was probably even greater than the per-visit data indicate. We also allowed up to four visits by *Bombus* and found that the amount of pollen in androecia was only depleted to about 180 000 grains, well above the 100 000 grains left after one *Apis* visit (data not shown, least significant difference multiple comparisons, $P < .001$).

The net amount of pollen transferred at the two sites differed strikingly, significantly (Fig. 2), and in a fashion consistent with the results of individual visits and the difference in the visitor faunas between the two sites. In Patch 1 androecia were more thoroughly emptied of pollen than in Patch 2, being left with <50 000 grains as opposed to >150 000. And, ironically, stigmas in Patch 1 received much less pollen than in Patch 2, only a few grains vs. several hundred.

Discussion

The difference between our two sites in the types of animals visiting flowers translated into a marked contrast in the relationship between pollen removal and pollen deposition. Net pollen transfer was in accordance with the composition of the two visitor suites and the single-visit transfer components of the different bees. In Patch 1, where pollen collectors were dominant, more pollen was removed and less delivered than in Patch 2, where nectar-collecting *Bombus* was dominant. Pollen deposition in Patch 1 was, if anything, lower than might have been expected, given the presence of a few *Bombus.*

In the *Impatiens* system there is no necessary relationship between pollen removal and deposition. The simplest expectation—that high removal leads to high subsequent deposition (and high paternity)—is surely incorrect. Because pollen collectors remove lots of pollen but deposit very little of it, while *Bombus* removes less but deposits more, one might even expect a negative association between removal and subsequent deposition. This would be true if flowers were only visited once. Because flowers are visited many times, the situation is complicated by an effect of the sequence of visitors. A flower visited first by a *Bombus* and later by an *Apis* ought to have high removal and many of its grains transferred, whereas a flower visited first by an *Apis* and later by a *Bombus* ought to have high removal but few of its grains transferred. Across flowers, therefore, the amount of pollen removed might be only weakly (and negatively) correlated with the amount of pollen transferred to stigmas. Male reproductive success is determined by the transfer characteristics—both removal and deposition—of all the visitors. Pollen removal by itself should not be used as an estimator of paternal fitness when there is heterogeneity among floral visitors.

When *Bombus* is present, *Apis* and *Dialictus* are antagonists rather than mutualists of *Impatiens.* They effect very little pollen transfer, and flowers visited by these pollen collectors are prevented from having their pollen transported by *Bombus.* Our results provide a counterexample to the generalization that pollen-collecting bees are more effective pollinators than nectar-collecting bees (Free 1970: 84–87).

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CANOPY STEREOGEOMETRY OF NON-GAPS IN TROPICAL FORESTS—A COMMENT

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Lieberman et al. (1989) present an interesting and novel way of looking at the light environment within a forest. It appears to be an especially useful technique for describing the niche of different species within that environment (as the authors have done for *Cecropia obtusifolia*), and for measuring changes in the light environment over time. However, they dismiss traditional methods based on the spatial delineation of gaps, and assume that light is the only factor affecting the growth and regeneration of tree species.

The following discussion will introduce other factors that need to be considered when utilizing the canopy stereogeometry method presented by Lieberman et al. (1989). A simulation model of different-sized gaps will be used to present the arguments for not shifting gap studies to an individual tree level focus.

The Methodology

The following comments on their methodology are being presented with the intent of improving the usefulness and stimulating further development of the technique. Lieberman et al. (1989) used 10 m as the limiting distance for inclusion of trees in the canopy-closure index (G) calculation. If used across a wide range of forests, however, this distance should vary depending on the height of the canopy. Defining a limiting distance based on a certain percentage of canopy height would allow the calculation to be consistently applied to forests of different statures. Ideally, the calculation should be made in such a way that a canopy-closure index of zero indicates that the sample point receives full sunlight for an ecologically meaningful period.

It may be more appropriate to use a limiting angle, rather than horizontal distance, for determining which trees should be included in the calculation. A tall tree 10.1 m from the sample point would have a greater shading effect than a shorter tree 9.9 m away, but would not be included under the present method. The use of a limiting angle would correct this problem. Furthermore, the use of a circular radius of inclusion is less appropriate in temperate and boreal zones, where shading is more directional. In such forests, it may be better to include only those trees to the south of the sample point, or to weight the trees according to their direction from the point.

Finally, shading from adjacent trees affects entire crowns, not just the highest point. A tree growing in an open field receives more sun than one that is closely crowded by other trees of equal height. Yet both trees would have a canopy-closure index of zero. Perhaps it would be better to calculate the average value of several points throughout the height of the crown of the sample tree. A realistic measure of the light environment faced by individual trees would require having more specific data on crown size and foliage distribution by tree species, and how these parameters vary with tree size and age and the changing light environment.

Distinguishing Gaps from Non-Gaps

The authors suggest moving to a tree-based rather than a gap-based approach to forest dynamics research because of the difficulty of defining closed forest (or "null gap") distinct from gaps. They state that the canopy-closure indices calculated by moving a "unit tree" along points on a grid are normally distributed, while the existence of distinct gaps should lead to a bimodal distribution.

However, this unimodal distribution is the result of the relatively small area covered by gaps. Data from Sanford et al. (1986) indicate that only ≈ 6% of the area of the La Selva forest in Costa Rica is in gaps >40 m^2. The distribution of values for points in these gaps will be different from those that fall in closed forest,

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