# COMPARISONS OF POLLEN REMOVAL AND DEPOSITION BY HONEY BEES AND BUMBLEBEES VISITING APPLE

Karen Goodell and James D. Thomson
Department of Ecology and Evolution
State University of New York, Stony Brook
New York 11794-5245,
USA

Abstract

The relative values of pollinators to crops depend on how much pollen they remove from anthers as well as how much they deposit on stigmas. On apples, *Apis* workers and *Bombus* queens differ in both pollen deposition and removal because they frequently adopt different foraging behaviors. Nectar-collecting *Apis* removed fewer pollen grains from the anthers of cv Delicious than did nectar- and pollen-collecting *Bombus*. On cv Rome, *Apis* deposited fewer grains on stigmas than *Bombus*, but removed equivalent amounts.

## 1. Introduction

The number of grains actually delivered by pollinators from a flower that receives a certain visitation regime is one way of quantifying the effectiveness of different pollinators, and bears on evolutionary questions such as sex allocation, pollinator attraction, and optimal pollen presentation schedules. Most workers have compared the quality of different insect species as pollinators by assessing the performance of each species separately. When different species of insects covisit flowers, however, complicated interactions between them make it hard to determine which species is most valuable in pollinating the plant. Simulation models of pollen depletion can clarify these interactions if one knows: (1) the number of visits, (2) the amount of pollen removed, (3) the amount of pollen delivered (ideally as a function of pollen removed), and (4) pollen presentation schedules (Harder and Thomson 1989, Thomson and Thomson 1992). These data allow one to estimate the amount of pollen delivered to stigmas as a function of the amount removed (e.g., using simulation package "Bee Visit" [available from JDT]). Such estimates have important implications for the pollination of agricultural crops with chronically low seed set (and outcrossing plants in general).

An insect that delivers many pollen grains (high D) is usually considered to be a better pollinator than one that delivers fewer (low D). Insects that remove more pollen grains (high R) should also be better, especially for plants with poricidal anther dehiscence, for which getting pollen into circulation is likely a limiting factor in male reproductive success. What really matters, however, is both of these quantities at once, along with the visitation rate to the flower.

Consider a pollinator represented as a point on axes showing the amount of pollen removed by a single visit to a flower and the amount of that pollen that is deposited on the stigmas of other flowers (Fig. 1). Complete delivery is unlikely because pollen is lost during transfer or removed from circulation by the pollinator. In Fig. 1a, A is a better pollinator per-visit than B because it deposits more of the pollen that it removes than B. In Fig. 1b, B is a better pollinator per-visit than A because it is both high D and high R (processes more grains), but this difference might be offset if A were more abundant. In Fig. 1c, A and B would be equivalent if only a single visit occurs because they both deliver the same amount of pollen to other stigmas, but if multiple visits occur, A would be better than B because B will take more pollen out of circulation and reduce the amount

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of pollen available for subsequent visits. If many visits occur, A may be *much* better than B if A is a high D, low R pollinator and B is a low D, high R pollinator (Fig. 1d).

Thus, the value of a particular pollinator depends on how many visits are expected, and how much pollen is left behind to be taken in later visits. Simulations using Bee Visit that include these factors indicate that low D bees can be functional mutualists in the absence of high D bees, but they can be functional parasites when high D bees are also in the system (Thomson and Thomson, 1992).

Real pollination systems can be affected by these differences in delivery and removal by visitors. Wilson and Thomson (1991) reported that *Apis* visiting *Impatiens capensis* flowers primarily collect pollen and seldom visit female-phase flowers (they do not make contact with the stigmas even if they do). *Bombus*, in contrast, usually feed for nectar from these flowers, removing less pollen from anthers and delivering more pollen to stigmas than *Apis*. When *Apis* collected nectar they did not differ from *Bombus* in removal and deposition, but such behavior was rare. Therefore, *Apis* acted as a pollen parasite in this system.

We report the initial results of work that examines the efficiency of *Apis* and *Bombus*, and their interactions in pollinating apples, *Malus sylvestris* Mill. We initially expected that *Apis* and *Bombus* would differ because of reports of "sideworking" by *Apis*, especially on cv Delicious (McGregor, 1976). The filaments of apple stamens restrict access to the nectaries by short-tongued *Apis*, requiring them to insert their head and thorax into the column of stamens to reach the nectaries. Particularly on Delicious, some individuals collect nectar by reclining sideways on the petal and inserting their proboscises between the anther bases, allowing them to work around the flower without much contact with the stigmas. In contrast, pollen-collecting *Apis*, and both nectar and pollen-collecting *Bombus* (queens) approach flowers from above, landing directly on the anthers and stigmas.

## 2. Materials and methods

We measured pollen removal and deposition by *Apis* and *Bombus* on four varieties of apples: Delicious, MacIntosh, Empire, and Rome (although we lump our results for MacIntosh and Empire because of difficulty distinguishing them in the field) at a commercial apple orchard in Northport, Long Island, New York in May, 1996. Flowers opened in screen boxes on the trees to ensure virgin flowers, which were then offered to foraging *Apis* and *Bombus*. A single visit to each flower was timed and classified as nectar-collecting, pollen-collecting, nectar-and-pollen collecting, or sideworking. After the single visit, we separated the dehisced and undehisced anthers into vials and made stigma squashes on slides dabbed with fuchsin-tinted glycerine jelly. Flowers were presented either intact or (on Rome only) emasculated in bud.

The number of pollen grains remaining in dehisced anthers and in undehisced anthers was counted using an Elzone 280-PC particle counter. We estimated the number of pollen grains removed per dehisced anther by subtracting the amount remaining per dehisced anther of each sample from the average number of grains per undehisced anther of that variety. We also counted the number of pollen grains deposited on stigmas. Comparisons of deposition and removal by *Apis* and *Bombus* were made using non-parametric statistics (Mann-Whitney U and Kruskal-Wallis tests).

## 3. Results

*Bombus* tended to make shorter visits than *Apis* (median = 1.27 s, upper quartile = 1.71 s, lower quartile = 1.0 s for *Bombus*, and median = 4.90 s, UQ = 7.49, LQ = 3.36 for *Apis*, $p<0.001$), but because there was no clear relationship between the time spent at a flower and the amount of pollen either removed or deposited, we did not take the time of visit into account in the following analyses.

Pollen counts per anther differed among the varieties: Delicious (median = 7463/anther, UQ = 10339, LQ = 3467) > Rome (median = 7411, UQ = 7980, LQ = 6760) > Mac/Empire (median = 4492, QU = 7980, LQ = 3008) ($p<0.05$, Kruskal-Wallis) and variation among anthers within flowers was high. On average, *Apis* and *Bombus* removed 25% and 35% of the available pollen from Delicious, 29% and 26% from Mac/Empire, and 45% and 48% from Rome, respectively. *Apis* and *Bombus* did not differ in their removal of pollen when all types of visits were considered within varieties or when we considered each visit type separately for all varieties. In fact, the only difference between *Apis* and *Bombus* in pollen removal was found for nectaring bees on Delicious (Fig. 2a). *Apis* removed a median of 1844 grains (UQ = 3129, LQ = 523) compared to a median of 2713 grains (UQ = 3370, LQ=1911) removed by *Bombus* ($p<0.05$). Approximately 50% of the *Apis* nectar visits to Delicious were sideworking. If sideworking visits are omitted from analysis, *Apis* and *Bombus* no longer differ in removal: the difference in removal by these two bees is caused by sideworking in *Apis*, which only occurred frequently on Delicious.

Stigmas of intact flowers had high pollen counts, probably because a large amount of self pollen was knocked onto the stigma during the visit. The stigmas of emasculated flowers (done only on Rome) visited by *Apis* had a median of 55 grains (UQ = 79, LQ = 29), significantly fewer than the median of 153 grains (UQ = 225, LQ = 95) deposited on those visited by *Bombus* ($p<0.001$, Fig. 2b). Few bees attempted to visit emasculated flowers for pollen, as might be expected, so the differences between deposition by *Apis* and *Bombus* largely reflects the behavior of nectaring bees.

## 4. Conclusions

Our results suggest that *Bombus* and *Apis* differ in pollen deposition and removal in some circumstances, but that these differences are mainly associated with the behavior the bees adopt, and in the case of Delicious, the particular morphology of the flower. *Apis* and *Bombus* appear to be equally effective as pollinators when collecting pollen, although we may lack power to detect true differences because of small sample sizes. Nectaring *Apis* and *Bombus* most likely differ in character as pollinators because *Apis* can sidework without contacting the sexual parts of the flower, and also because *Apis* are smaller than *Bombus* queens and passively carry off fewer pollen grains. We lack sufficient data on pollen deposition for Delicious to rigorously test potential interactions between *Apis* and *Bombus*. If, however, *Apis* and *Bombus* are equivalent, then *Apis* could be a superior pollinator if flowers receive multiple visits. If *Bombus* deposits more than *Apis*, as we might predict based on our observations, then *Bombus* would be the better pollinator, but we would not predict unfavorable interactions between the two pollinators.

On Rome, deposition data show that *Bombus* deposited more grains than *Apis*, despite the fact that *Apis* rarely sideworked on Rome. Our data on removal from Rome indicate no statistically significant differences between *Apis* and *Bombus* (although the sample sizes are low for these means). These results suggest that *Apis* is a poor pollinator relative to *Bombus* because it deposits fewer grains of those it removes relative to *Bombus*. Our model of pollinator interactions predicts that mixtures of *Apis* and *Bombus* on Rome result in less efficient pollination than *Bombus* alone. In this study we did not attempt to measure the amount of the pollen removed from a flower that reaches the stigmas of other flowers because it requires a more complicated design. This type of data is important in creating more realistic models. Better models will also require inclusion of the different working speeds of the bees - *Bombus* is at least four times faster than *Apis* - and their different propensities to move between trees.

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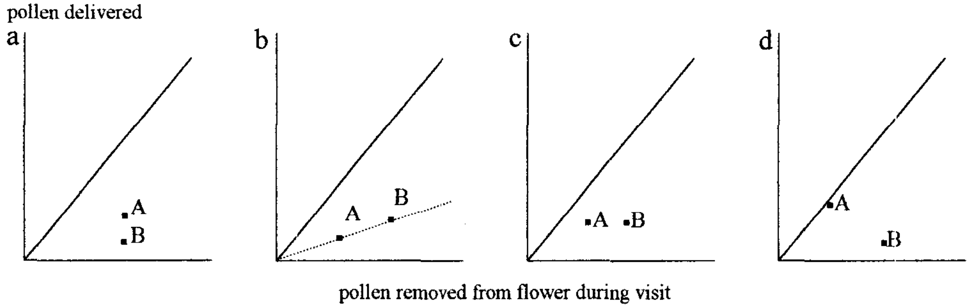


Figure 1. Pollinators represented as points on the axes pollen removed from a flower during a single visit versus the amount of that pollen that is deposited on the stigmas of other flowers. The solid lines represent complete pollen delivery.

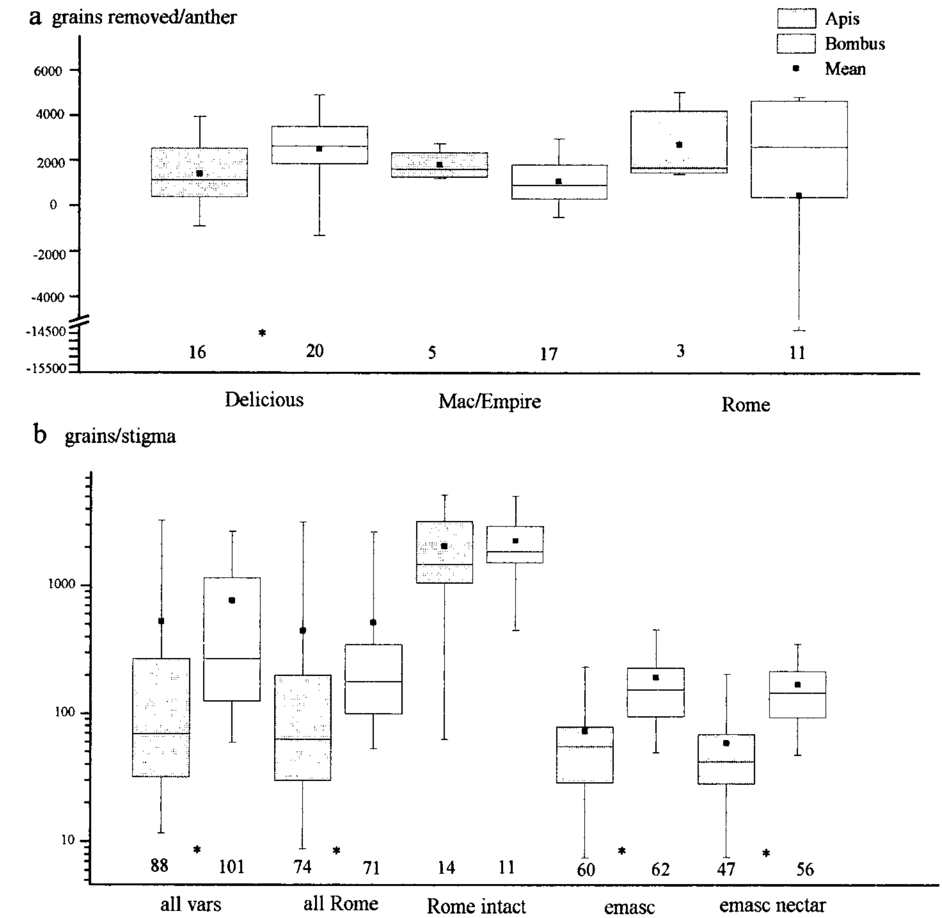


Figure 2. Box plots showing medians and interquartile ranges of pollen removal and deposition by *Apis* and *Bombus* on apple. (a) Number of pollen grains removed per dehisced anther by nectaring bees for three varieties. (b) Number of grains deposited (log scale) per stigma for all varieties (all vars), all visits to Rome (all Rome), visits to emasculated Rome (emasc), nectar visits to emasculated Rome (emasc nectar). Asterisks indicate significant differences ($p$<0.05). Numbers below boxes indicate sample sizes.