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Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers

JAMES D. THOMSON* and KAREN GOODELL†
Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794–5245, USA

Summary

1. To help evaluate the worth of alternative pollinators in agriculture, we present a theoretical framework for comparing the effectiveness of two or more pollinators by measuring pollen removal and deposition.
2. We report pollen removal and deposition data by *Apis mellifera* and *Bombus* spp. during single visits to four cultivars of apples (Golden Delicious, Starkrimson Delicious, Empire/MacIntosh and Rome) and Mission almond.
3. *Apis* and *Bombus* removed similar amounts of pollen from apple flowers but *Bombus* deposited more pollen on stigmas. Pollen-collecting bees removed more pollen from apple anthers than nectar-collecting bees. *Apis* that approached nectaries laterally deposited substantially less pollen than other visitors.
4. *Apis* and *Bombus* removed and deposited similar amounts of pollen on almond flowers. *Apis* tended to remove more during pollen-collecting visits than nectar-collecting visits. The type of resource sought did not significantly influence deposition.
5. Based on removal and deposition data, additions of *Bombus* may increase pollen delivery in apple orchards but reduce pollen delivery in almond orchards if *Apis* already serve as primary pollinators. Additional data on inter-tree and inter-row flights would be necessary to know how much these changes in pollen transfer might affect fertilization.
6. Measures of pollen-transfer effectiveness do not provide a complete assessment of pollination value, but can serve as a general, inexpensive tool for pre-screening possible alternative pollinators.

Key-words: orchard crops, pollen transfer, pollination, pollinator behaviour, pollinator effectiveness.

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Introduction

COMPARING POLLINATORS

Despite the pre-eminence of honeybees *Apis mellifera* L. as managed agricultural pollinators, other insects are more effective in certain situations. Examples include *Megachile rotundata* as a pollinator of alfalfa *Medicago sativa* (Stephen 1962; Bohart 1972) and bumblebees *Bombus* spp. for pollination of tomato *Lycopersicon esculentum* in greenhouses (de Ruijter 1997). Proponents of alternative pollinators believe that further research will produce more such successes (Parker, Batra & Tepedino 1987; Cane 1997).

We agree that further exploration is desirable, but developing and testing a new pollinator is expensive. Pollen presentation theory (PPT; Harder & Thomson 1989; Thomson & Thomson 1992) suggests that simple measurements of pollen removal and deposition can help decide whether a particular alternative pollinator is worth investigating further. PPT also shows that previous approaches for comparing pollen-transfer effectiveness are potentially flawed because they do not address the depletion of pollen from anthers. We present pollen removal and deposition data for bumblebee and honeybee pollinators of cultivated apples *Malus domestica* Borkh and almonds *Prunus dulcis* (P. Mill.) D. A. Webber, and discuss their implications for the relative values of these two insects as pollinators. Growers of orchard crops have long been concerned about inadequate pollination (Williams & Wilson 1970; Kendall 1973), and recent studies have compared alternative pollinators (Torchio & Asensio 1985; Bosch & Blas 1994; Freitas 1995). When honeybees are in short supply, such as during

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*Present address and correspondence: Department of Zoology, 25 Harbord St, University of Toronto, Toronto, Ontario, Canada M5S 3G5 (e-mail jthomson@zoo.toronto.edu).
†Present address: Department of Ecology, Evolution and Natural Resources, Rutgers University, Cook College, New Brunswick, NJ 08903, USA.

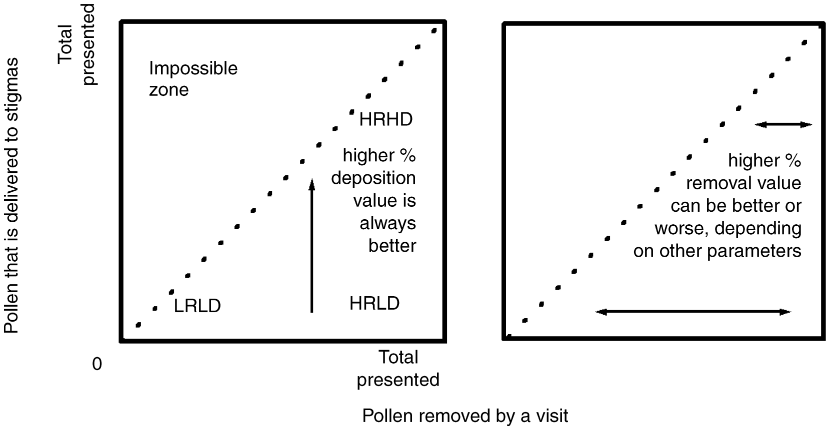

Fig. 1. Pollinators represented as points in bivariate space defined by the amount of pollen they remove from flowers and the amount of that pollen that is subsequently delivered to the stigmas of recipient conspecific flowers. L, H = low, high; R, D = removal, deposition. The broken lines represent complete pollen delivery.

the recent outbreak of mite parasites (Watanabe 1994), alternative pollinators may be important. In addition, some have suggested that honeybees are ineffective on certain apples because they visit the flowers without contacting the stigmas (Roberts 1945; McGregor 1976; Robinson 1979; Benedek & Nyéki 1996). We compared pollen transfer by honeybees and bumblebees in apples and almonds.

POLLEN DEPLETION MODELS

Models of pollen transfer (Thomson & Thomson 1992; Thomson & Thomson 1999; see also Harder & Thomson 1989; Young & Stanton 1990; Harder & Wilson 1997; LeBuhn & Holsinger 1998) hinge on pollinator-specific rates of pollen removal from anthers and deposition on stigmas. Because pollen removed by one pollinator is no longer available for another to deliver, different pollinators interact in complex non-additive ways. The interplay between removal and deposition can be grasped by envisioning pollinators as occupying a location in 'removal–deposition' space (Fig. 1). The left panel indicates the positions of three hypothetical pollinator types: low removal–low deposition (LRLD), high removal–low deposition (HRLD) and high removal–high deposition (HRHD).

Although it wastes much pollen (for example through grooming), a HRLD visitor will transfer some pollen to stigmas. Therefore, its visits will benefit the host-plant, as long as no better pollinator is available. If a HRHD visitor also visits the population, however, HRLD visits can reduce overall pollen transfer. The HRLDs parasitize the plants by diverting grains that would otherwise be delivered by HRHDs. If two visitors remove equal amounts of pollen, the one with a higher delivery rate is always a superior pollinator; if they remove different amounts, which one is better depends not only on deposition rates but on other variables, including the schedules of pollen presentation and visitation (Fig. 1; Thomson & Thomson 1992).

When pollen depletion is considered, then the pollination value (in terms of its per visit pollen transfer dynamics) of a particular species becomes context-dependent. Importantly, this context dependence cannot be deduced from comparative data on pollen delivery alone unless one does a factorial experiment in which replicate plant populations are exposed to many combinations of numbers of visits by the two types of pollinator. The practical difficulty of conducting such experiments prompted the alternative approach that we used. By measuring both pollen removal and deposition by different visitors, we can at least determine whether a pair of pollinators differs sufficiently to warrant further investigation. If so, we advocate further experiments that establish the conditional dependence of pollen delivery on pollen removal combined with modelling the pollination potential of various mixtures of visitors.

Materials and methods

APPLES

In our study orchard (Northport, New York, USA; 40°54′13″ N, 73°20′44″ W), apples bloom when bumblebee queens are foraging. Worker bees appear as flowering wanes. Commercial growers typically provide honeybees for pollination.

Throughout flowering in 1996–97, we counted pollen grains deposited on stigmas and estimated pollen removed from anthers following single visits to virgin flowers. We isolated branches (Starkrimson Delicious, Golden Delicious, Empire, MacIntosh or Rome varieties) in rigid screen cages with plastic covers. Flowers opened normally, protected from jostling, insects and rain. Flowers used to quantify deposition were emasculated in bud because heavy self-deposition hampered stigma counts.

Between 09:00 and 16:00 on fair days, we removed open flowers, attached them to a 0·5-m rod, and offered them to foragers. Flowers used to estimate pollen removal averaged 11·1 dehisced and 7·2 undehisced anthers. We timed each visit by stopwatch, noting the visit type (pollen or nectar collection, frontal or lateral approach), presence or absence of pollen loads, and grooming.

Pollen removal

After a visit, we removed dehisced and undehisced anthers with fine forceps and placed them into separate vials, working over the vials to avoid loss. We recorded the number of anthers, discarding deformed or half-dehisced ones. We left the undehisced anthers in uncapped vials until dehisced, then added 70% ethanol.

We estimated the number and size distribution of grains in each vial using an Elzone 280-PC electronic particle counter (Micromeritics, Norcross, GA) with a 150-µ orifice. We added 1% aqueous NaCl, sonicated each sample for 20 s at 9 watts with a Virsonic wand (VirTis Inc. Gardiner, NY) to suspend the grains, and counted three 1-ml subsamples, shaking the vial between counts. We determined the volume counted by weighing vials before and after, then converted the raw counts to a density, and finally multiplied by the total volume of sample. We counted all particles between 16·85 and 43·71 µ except for samples with bimodal distributions. All samples contained very small particles, perhaps dust or stray cells. If we encountered two well-defined peaks that were clearly not 'dust', we extended the lower range to 13·04 µ diameter. The second, lower, mode was consistent across all bimodal samples, and may represent undeveloped pollen grains.

The average number of pollen grains per undehisced anther provided an estimate of the total pollen available per anther before the flower was visited. From that number we subtracted the average number of pollen grains per dehisced anther to estimate the number of grains removed per anther.

No. grains removed/anther = No. grains/undehisced anther – No. grains/dehisced anther

Pollen deposition

After a visit by either an *Apis* or a *Bombus*, the stigma of an emasculated experimental flower was removed with clean forceps and placed into a drop of melted glycerine jelly tinted with basic fuchsin on a microslide. We applied gentle pressure to the top of a cover slip to distribute the pollen grains into a monolayer. Every grain was counted at 200× magnification under a Leitz compound microscope.

Visitor behaviour

Most bees approach apple flowers directly, landing on the centre of exserted reproductive parts. They actively collect pollen by scrabbling at the anthers with their legs. Some actively tongue-probe for nectar, which collects at the apex of the ovary, inside a tight ring of filaments. On a single visit, they may do either or both activities.

Some individual honeybees adopt a particular posture in the course of visiting flowers for nectar. A 'sideworking' bee feeds by standing on a petal facing the flower's centre, lowering its head below the outer fringe of anthers, and inserting its proboscis directly through the phalanx of filament bases to reach the nectary from the side. Some have hypothesized that this posture reduces pollination success, because a sideworking bee will make only peripheral contact with the anthers and none with the stigmas (McGregor 1976 and references therein). Some varieties (for example Golden Delicious, Spygold and Téli aranyparmen) are more susceptible to sideworking than others, probably because they produce a looser staminal phalanx (Roberts 1945; Benedek & Nyéki 1996).

Because sideworking might strongly affect pollen transfer, we not only measured pollen removal and deposition for sideworking visits (above), but conducted some brief observations to assess the frequency of this behaviour. On 11 May 1997, 28 April and 3 May 1998, observers spent 15-min periods at various times of day walking along rows of particular varieties and scoring bees by the following rules. On arriving at a tree, locate a honeybee. Follow it to its next flower, and score the behaviour as either a sideworking nectar visit (described above), a frontal visit for nectar and/or pollen, in which the bee perches directly on the spray of anthers and stigmas, or a mixed visit that combined both elements. Mixed visits most commonly occurred when a bee started by sideworking, then left the flower by passing over the reproductive organs.

ALMONDS

We conducted the almond study at the University of California Bee Laboratory at Davis, California, USA (38°33′18″ N, 121°44′09″ W) in February 1997, where nearby almond orchards were in bloom. All of the data collected used the Mission variety of almond. We used similar methods as above, except as noted. Bumblebees were rare, partly because almonds bloom before most queens have emerged, and partly due to the large numbers of honeybee hives present in the area, which may have discouraged other bees. To obtain enough visits, we enclosed foraging bees and flowers on cut almond branches in a 2·5 × 2·5 × 2·5-m screen picnic tent with an opaque top. One small colony ('nucleus') of honeybees and one commercial colony of bumblebees *Bombus terricola occidentalis* (Greene) provided foragers. Therefore, our bumblebee visits to almonds were by worker bumblebees, whereas those to apples were by queens. Although this difference reduces the comparability of the two studies, an almond grower interested in bumblebee pollination would certainly need to supply colonies, whereas an apple grower might simply try to encourage wild queens.

We stocked the flight cage with bouquets of hybrid almonds that grew around the laboratory. We renewed these every morning with freshly cut branches kept in buckets of water. Data were collected between 09:00 and 14:00; by afternoon, stocked flowers were depleted and the bees' foraging patterns could not be considered representative of free-foraging bees. We kept cut branches of Mission variety almonds in buckets of water in the laboratory as a source of test flowers. Flowers that had opened overnight were removed from the branches minutes before offering them to a foraging bee. The test flowers had comparable nectar quantities to newly opened flowers in the field (K. Goodell, personal observation). These branches were replaced with freshly cut branches each evening.

Results

APPLES

Visitor behaviour

Visits by *Apis* and *Bombus*, while foraging on trees and visiting experimental flowers, varied greatly in duration. Part of this variation appeared to be associated with the type of visit, with sideworking taking longer than frontal visits in *Apis*. *Bombus* consistently worked flowers on the order of three- to fourfold more quickly than *Apis* (Table 1). Both bee taxa tended to make longer visits to experimental flowers than to background flowers of either apples or almonds (Table 1), probably because the experimental flowers had larger amounts of nectar and pollen than the background forage. We found no significant relationship between the length of a visit and the amount of pollen deposited or removed for any combination of bee and flower species (unpublished data set).

We combined the frequency of *Apis* visits over days and years for three types of visits: sidework, mixed and frontal. We used contingency tables to test for independence of visit type and the time for day for those apple varieties for which we had enough data: Starkrimson Delicious and Golden Delicious. For these analyses, the time classes depended on the available data, but spanned a period between 09:30 and 16:30. There was no interaction between visit type and time for Golden Delicious (chi-square = 6·19, d.f. = 8, $P > 0·05$). Time of day affected visit type in Starkrimson (chi-square = 21·23, d.f. = 18, $P < 0·05$): less sideworking in the morning and more in the afternoon.

Delicious varieties are thought to promote sideworking by honeybees because their stamens are loosely packed. We tested the influence of variety on visit type using a contingency table analysis. Because we observed visits on all varieties with equal intensity for morning and afternoon hours, we combined visit frequencies over times of day for this analysis. We also combined MacIntosh with Empire because of low sample sizes for MacIntosh and their similar floral structure. The frequency of sideworking varied significantly with tree variety (chi-square = 70·54, d.f. = 6, $P < 0·001$). As proposed, the heterogeneity in visit types arose from more sideworking on the two delicious varieties: Starkrimson and Golden Delicious (Fig. 2). *Apis* sideworked Golden Delicious more often than Starkrimson Delicious (proportion of sidework visits, Golden = 32% vs. Starkrimson = 20%).

Table 1. Mean (SD, *n*) visit lengths in seconds for *Apis* and *Bombus* on apple and almond flowers. Nectar includes frontal nectar visits only, pollen includes any visit during which bees actively collected pollen. *Bombus* foraging on apples were queens, and on almonds they were workers. Data for free foraging bees were collected during sunny weather: for almonds, on 18 February, 11:30–15:30, 12–22 °C; for apple, on 11 May, 09:00–16:00, 24–26 °C

	Apis	*Bombus*
Apples		
Free foraging 1996		
Nectar	4·99 (4·10, 22)	2·67 (2·79, 41)
Pollen	6·14 (4·53, 34)	1·69 (0·73, 12)
Side	6·43 (4·48, 48)	
Total	5·94 (4·42, 106)	1·55 (0·85, 56)
Experimental flowers 1996		
Nectar	8·82 (5·74, 32)	2·59 (1·67, 94)
Pollen	8·00 (7·54, 35)	3·15 (1·78, 27)
Side	10·55 (8·21, 35)	
Total	9·00 (7·27, 105)	2·74 (1·69, 124)
Experimental flowers 1997		
Nectar	14·81 (9·94, 40)	3·93 (3·55, 78)
Pollen	15·15 (7·95, 52)	8·11 (8·13, 22)
Side	18·07 (11·14, 34)	
Total	15·71 (9·40, 127)	5·23 (6·38, 103)
Almonds		
Free foraging (in tent)		
Nectar	12·31 (13·18, 19)	16·02 (17·49, 8)
Pollen	12·96 (10·95, 13)	5·22 (2·48, 13)
Total	12·57 (12·14, 32)	9·34 (11·82, 21)
Experimental flowers		
Nectar	21·90 (21·12, 19)	25·63 (31·20, 6)
Pollen	23·97 (20·66, 28)	10·35 (7·53, 46)
Total	22·66 (20·68, 48)	12·11 (13·03, 52)

Pollen removal

The pollen removal data collected in 1996 were from Starkrimson Delicious, Empire, MacIntosh and Rome variety apples. In 1997 we concentrated our efforts on the Rome variety. We quantified removal in two ways: the number of pollen grains removed per anther, and the proportion of available pollen removed. However, a strong positive correlation between the number of pollen grains available and the number removed (Fig. 3a), and the significant variation in pollen availability between flowers, made the proportion removed the more suitable comparison. Therefore, we report statistical analyses for the proportion of pollen removed only. In addition to comparing removal between bees, we also contrasted visit types (nectar, pollen, sideworking) within bee types, because the position and

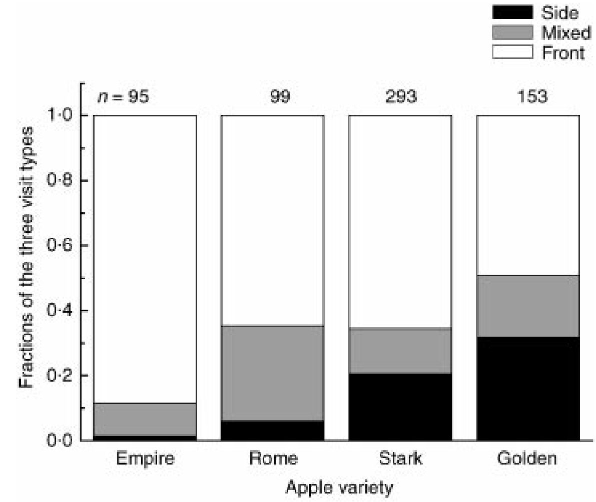

Fig. 2. The proportion of sideworking, frontal and mixed (side and front) nectar-collecting visits made by *Apis mellifera* visiting different varieties of apple: Empire (combined MacIntosh and Empire), Rome, Starkrimson and Golden Delicious. Data are combined from 15-min intervals over several days. Sample sizes above each bar.

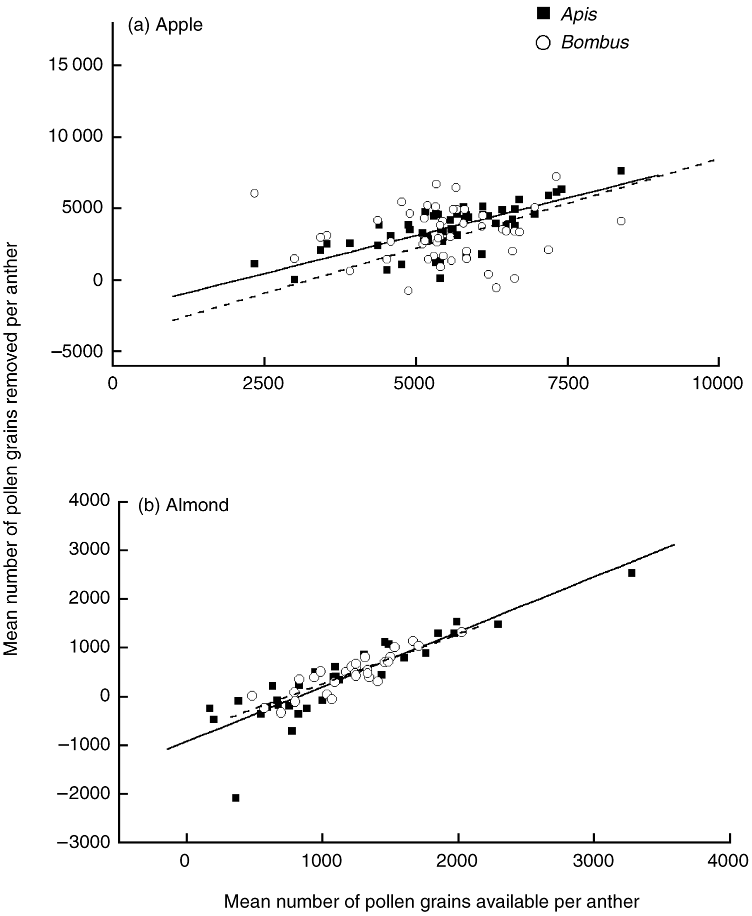

Fig. 3. The mean number of pollen grains that *Apis mellifera* and *Bombus* spp. removed per anther following a single visit to a previously unvisited flower as a function of the mean number of pollen grains available per anther. Linear regression lines are solid for *Apis*, dashed for *Bombus*. (a) Apple flowers. *Apis*: removal = −2200·15 + 1·06(available); correlation coefficient $r = 0{\cdot}72$, $n = 55$, $P < 0{\cdot}0001$; *Bombus*: removal = −3597·92 + 1·17(available); $r = 0{\cdot}70$, $n = 49$, $P < 0{\cdot}0001$. (b) Almond flowers. *Apis*: removal = −936·90 + 1·13(available); correlation coefficient $r = 0{\cdot}88$, $n = 32$, $P < 0{\cdot}0001$; *Bombus*: removal = −767·42 + 1·02(available); $r = 0{\cdot}89$, $n = 29$, $P < 0{\cdot}001$.

behaviour adopted by foraging bees is likely to influence the amount of pollen removed (Freitas 1995; Freitas & Paxton 1998; Goodell & Thomson 1998).

We tested the effects of bee type and visit type on the proportion of pollen removed from apple anthers with two-way analyses of variance using PROC GLM in SAS because the sample sizes differed among factors (SAS 1985). For most of the removal data sets, the proportional data deviated from a normal distribution even after we applied an arcsine-square root transformation. Therefore, we converted the proportions to ranks for the analysis. Because foraging behaviour and variety appeared to be associated, at least for *Apis*, which primarily made sideworking visits to Delicious varieties, and because there were insufficient data for each bee on each variety, we did not include variety as a factor in the ANOVA. We examined the differences among varieties in the amount of pollen removed in another analysis by lumping visit types and using Kruskal–Wallis tests. The 1997 data included only Rome flowers.

The 1996 and 1997 data had different levels of visit type. In the full analysis of the 1996 data, we combined frontal and sideworking *Apis* nectar visits (= nectar) because *Bombus* did not sidework. The 1997 data included the visit type levels nectar, pollen and both (nectar and pollen). We explored the differences among levels within the factor visit type using contrasts. Depending on the levels present in the particular analysis, we contrasted pollen-only visits with nectar-only visits, pollen-only visits with both visits, and sideworking visits (*Apis*) with all other visit types.

In both years, visit type was significant but bee taxon was not (Tables 2 and 3, and Fig. 4). In 1996, there was a significant bee type × visit type interaction (Table 2). Therefore, the effects of visit type were analysed separately for each bee type in the 1996 data set. One-way ANOVA revealed a significant effect of visit type on pollen removed by *Apis* but not by *Bombus* (Table 2b). Contrasts showed further that sideworking *Apis* removed significantly less pollen than frontal visitors, and that frontal nectar collectors removed less pollen than pollen collectors (Table 2b). In 1997, bee type and visit type did not interact in determining removal from Rome flowers (Table 3). Contrasts revealed that nectar-collecting bees removed significantly less pollen than pollen-collecting bees, and bees collecting both resources removed the same amount as those collecting just pollen (Table 3).

Table 2. Analysis of variance on ranked proportions of pollen removed from apple flowers by *Apis* and *Bombus* for the 1996 data set. Factors are: (a) bee = the effect of bee taxon (*Apis* or *Bombus*), and visit = the type of floral resource collected (pollen or nectar); (b) visit = resource type and bee behaviour (pollen, nectar or sideworking nectar); and (c) visit = resource type (pollen, nectar or both)

Source	d.f.	MS	*F*	*P*
(a) All bees				
Bee	1	892·66	1·03	0·313
Visit	1	10123·70	11·66	0·001
Bee × visit	1	3454·45	3·98	0·049
Error	100	868·31		
(b) *Apis* only				
Visit	2	5996·46	10·25	0·001
Error	40	585·06		
Contrasts				
Sidework vs. rest	1	4617·85	7·89	0·008
Pollen vs. nectar	1	5926·26	10·13	0·003
(c) *Bombus* only				
Visit	1	976·93	0·92	0·343
Error	59	1066·67		

Table 3. Analysis of variance of ranked proportions of pollen removed from Rome apples for the 1997 data set. Factors are: bee = bee taxon (*Apis* vs. *Bombus*) and visit = type of floral resource collected (pollen, nectar or both)

Source	d.f.	MS	*F*	*P*
Bee	1	156·00	0·22	0·643
Visit	2	7223·39	10·00	0·0001
Bee × visit	2	1965·09	2·72	0·070
Error	96	722·09		
Contrasts (visit)				
Pollen vs. nectar	1	4078·70	5·65	0·020
Both vs. pollen	1	827·95	1·15	0·287

The removal data for 1996 included apple flowers of four varieties (Starkrimson Delicious, Empire, Rome and MacIntosh). Kruskal–Wallis tests indicated significant variation in the proportion of pollen removed from different varieties. If we disregarded Empire, for which we obtained only two *Apis* visits, *Apis* removed the least from Delicious flowers, probably due to a high proportion of sideworking visits, and removed the most from Rome ($H = 10·0$, d.f. = 2, $n = 14, 8, 21$ for Rome, Macintosh and Delicious, respectively, $P < 0·01$; Table 4). *Bombus* removed the least pollen from MacIntosh and the most from Rome ($H = 8·2$, d.f. = 2, $n = 10, 11, 23$ for Rome, MacIntosh, Delicious, respectively, $P < 0·02$; Table 4).

Pollen deposition

Most bees visited the emasculated flowers for nectar only, but a few scrabbled at the stamens as if trying to collect pollen. We therefore categorized a pollen visit as any visit during which the visitor scrabbled at the anthers, whether or not nectar was collected in addition. We present data for Rome (1996) and Golden Delicious (1997). Data for Delicious included sideworking by *Apis*, but not by *Bombus*. Because the deposition data were not normally distributed, we conducted non-parametric Mann–Whitney *U*-tests and Kruskal–Wallis tests to compare bees and visit types.

Bombus deposited more pollen grains on Rome stigmas than *Apis* (1996 data) ($U = 595·0$, $n = 60$ for both *Apis* and *Bombus*, $P < 0·0001$; Fig. 5a), mainly during nectar visits ($U = 188$, $n = 26, 54$ for *Apis* and

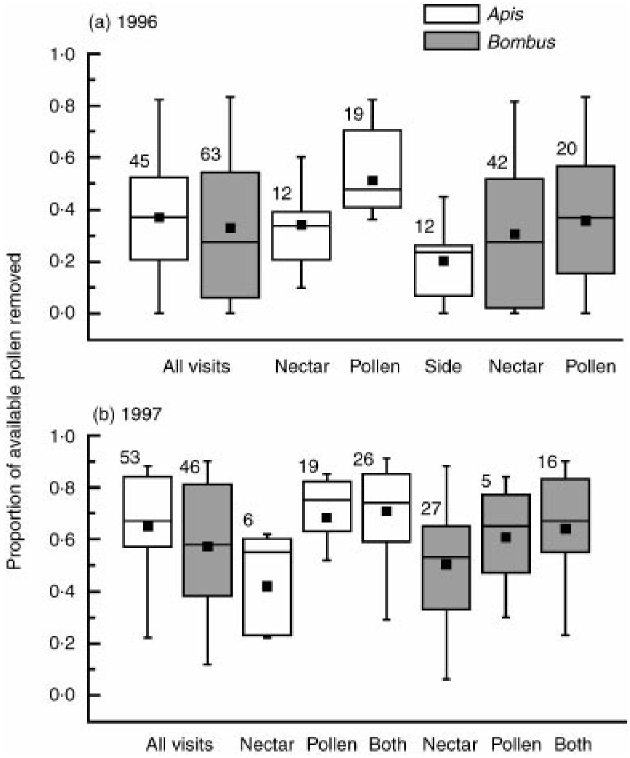

Fig. 4. Box plots showing the proportion of available pollen grains removed from previously unvisited apple flowers by *Apis mellifera* and *Bombus* spp. The bottom and top edges of the rectangle are the 25th and 75th percentiles, the horizontal line through the rectangle is the median, the solid square is the mean, and the tips of the whiskers indicate the fifth and 95th percentiles. The numerals on the boxes are the number of flowers sampled. (a) 1996 data collected from Delicious, Empire, MacIntosh and Rome varieties for all visits combined (All visits) and for subsets of visits broken down by the type of reward collected and position adopted by the bee. Nectar includes nectar-only visits except for sideworking visits made by *Apis*, which fall under Side. Pollen visits include any visit during which the bee collected pollen from the anthers. Sample sizes (number of flowers that received a visit) are given for each category. (b) 1997 data for the Rome variety. Both means the bee collected both pollen and nectar.

Table 4. 1996 data for pollen removal from apple flowers of four varieties during single visits by *Apis* and *Bombus*. Medians with lower (LQ) and upper quartiles (UQ), as well as means and standard errors of the proportion of available pollen removed, are provided

	Apis			*Bombus*		
Variety	Median (LQ, UQ)	Mean (SE)	*n*	Median (LQ, UQ)	Mean (SE)	*n*
Starkrimson	0·26 (0·16, 0·40)	0·27 (0·04)	21	0·30 (0·03, 0·47)	0·28 (0·05)	23
Empire	0·23 (0.10, 0·36)	0·23 (0·14)	2	0·25 (0·17, 0·46)	0·32 (0·05)	17
Rome	0·41 (0·17, 0·50)	0·35 (0·07)	8	0·16 (0·01, 0·28)	0·19 (0·07)	11
MacIntosh	0·56 (0·38, 0·79)	0·56 (0·07)	14	0·71 (0·23, 0·89)	0·58 (0·12)	10

Bombus, respectively, $P < 0{\cdot}0001$; medians: *Apis* = 50, *Bombus* = 145; Fig. 5a). During pollen visits, *Apis* and *Bombus* deposited equally, but the samples were small (Fig. 5a). Within either *Apis* or *Bombus* we found no differences in deposition between visit types. Similarly, for Golden Delicious in 1997 (all visit types pooled), *Bombus* deposited more than *Apis* ($U = 1072{\cdot}0$, $n = 70$, 50 for *Apis* and *Bombus*, respectively, $P < 0{\cdot}0001$; Fig. 5b). Deposition by *Apis* was greater for nectar visits than for sideworking visits ($U = 19{\cdot}35$, $n = 24$, 28 for nectar and side, respectively, $P < 0{\cdot}0001$; Fig. 5b). In frontal nectar visits, *Apis* and *Bombus* deposited equivalent amounts ($U = 521{\cdot}0$, $n = 24$, 46 for *Apis* and *Bombus*, respectively, $P = 0{\cdot}60$; Fig. 5b), so sideworking by *Apis* accounted for the observed differences between bee taxa.

ALMONDS

Visitor behaviour

Bees foraging within the tent made mostly pollen-collecting visits or combined pollen- and nectar-collecting visits. *Bombus* especially showed this tendency. Both species typically approached flowers directly and reached the nectaries by inserting their heads into the staminal column from above, sometimes parting the filaments with their legs. This visiting behaviour almost

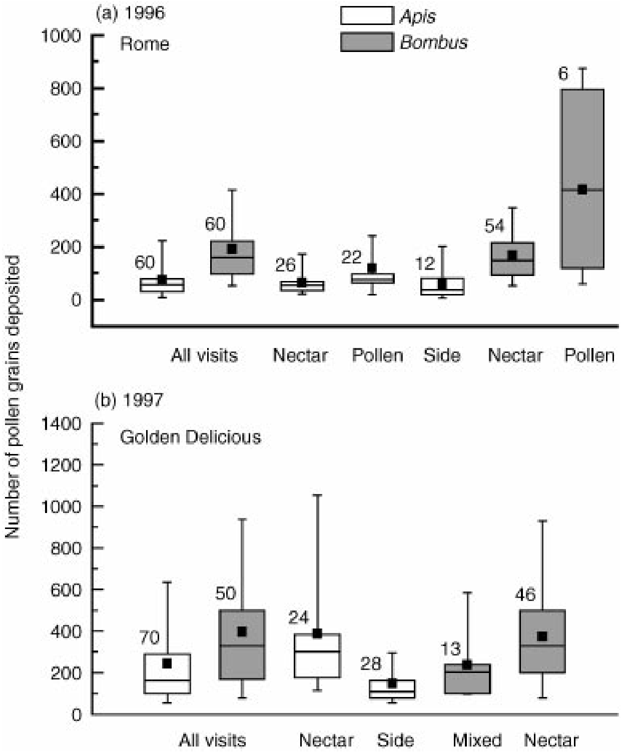

Fig. 5. The number of pollen grains deposited on apple stigmas during single visits by *Apis mellifera* and *Bombus* spp. (a) 1996 data for the Rome variety. (b) 1997 data for Golden Delicious. A mixed visit was a combination of sideworking and frontal nectar collecting. See Fig. 4 legend for explanation of terms and symbols.

always brought them in contact with the stigmas and anthers. *Apis* did not sidework. Even when honeybees approached the flower from the side, they usually would end the visit by climbing over the anthers. Of 30 nectar visits observed for *Apis*, both within the tent and free foraging, in only one case did the bee fail to contact the stigma. Both bee species typically collected pollen by scrabbling at the anthers, although *Bombus* would occasionally grasp the filaments and vibrate their flight muscles in an attempt to 'buzz' collect the pollen. As for apples, visit lengths varied substantially within bee species. On average, *Bombus* worked flowers 1·3–1·9-fold faster than *Apis*, although *Bombus* nectar visits were as slow or slower than those of *Apis*.

Pollen removal

As in apples, the amount of pollen removed by both *Apis* and *Bombus* varied positively with the amount of pollen available (Fig. 3b), so we report removal as proportion removed. The almond removal data were not normally distributed even after angular transformation. Therefore, we again used ANOVA on ranked proportions, with bee taxon and visit type as fixed independent factors.

Pollen removal varied greatly, ranging from 0 to 0·93 (*Bombus*) and 0 to 0·80 (*Apis*). Bumblebees tended to remove more, but not significantly so (Table 5 and Fig. 6). In contrast to the results for apples, removal was independent of the type of visit (Table 4). *Bombus* tended to remove more pollen than *Apis* during nectar-only visits, but we observed only two such visits from *Bombus*. These two visits appeared to have higher removal than pollen-collecting visits, which suggested that they may be unrepresentative. *Apis* and *Bombus* did not differ in how much pollen they removed per pollen visit ($U = 374{\cdot}5$, $P = 0{\cdot}80$, $n = 24, 29$ for *Apis* and *Bombus*, respectively; Fig. 6). *Bombus* typically buzz to release pollen from poricidal anthers (Buchmann 1983). On almonds, which do not have poricidally dehiscent anthers, buzzing did not increase pollen removal (Fig. 6; $U = 102{\cdot}50$, $P = 0{\cdot}16$, $n = 29, 8$ for pollen and buzz, respectively).

Table 5. Analysis of variance testing the effect of bee identity (*Apis* or *Bombus*) and type of floral resource collected (pollen or nectar) on the proportion of pollen removed from Mission almond flowers following a single visit. Nectar visits include nectar-only plus nectar with grooming. Pollen visits include pollen-only, pollen with nectar, pollen with grooming and buzz-collecting. Proportions were ranked for analysis

Source of variation	d.f.	MS	*F*	*P*
Bee	1	648·78	2·47	0·121
Visit	1	1·52	0·01	0·940
Bee × visit	1	924·21	3·52	0·065
Error	64	262·50		

Pollen deposition

Both *Apis* and *Bombus* deposited few grains per stigma, low compared with apples (Fig. 7), probably

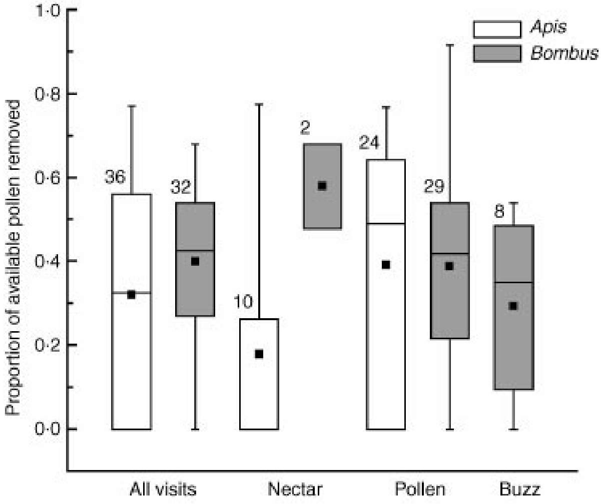

Fig. 6. The proportion of available pollen grains removed from previously unvisited Mission almond flowers by *Apis mellifera* and *Bombus occidentalis*. Buzz-collecting visits were made by *B. occidentalis* workers that grasped the anther filaments and vibrated their flight muscles to shake pollen from the anthers. See Fig. 4 legend for explanation of other terms and symbols.

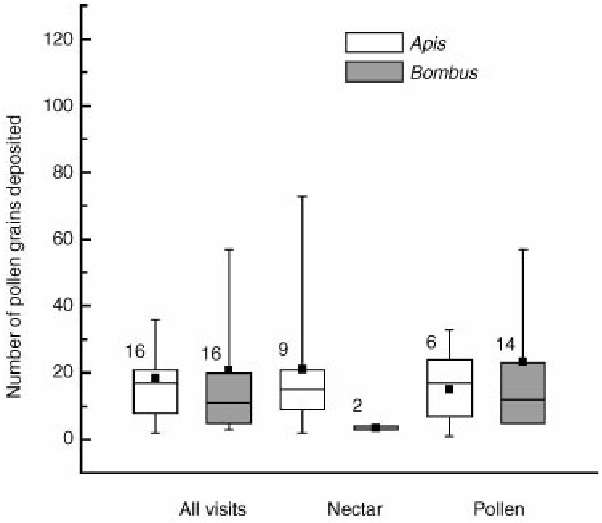

Fig. 7. The number of pollen grains deposited on Mission almond stigmas by *Apis mellifera* and *Bombus occidentalis* following single visits to emasculated flowers or flowers with no dehisced anthers. See Fig. 4 legend for explanation of terms and symbols.

because little pollen was available in the cage. Nevertheless, the data were comparable among bee species because they experienced the same environment while the deposition data were collected. *Apis* and *Bombus* deposited similar amounts of pollen on almond stigmas ($U = 148{\cdot}5$, $n = 16$ for both *Apis* and *Bombus*, respectively, $P = 0{\cdot}44$; Fig. 7). We found no evidence that the type of visit affected deposition of pollen.

Discussion

REMOVAL AND DEPOSITION

Apples

Apis and *Bombus* removed equivalent amounts, roughly half, of available pollen (Fig. 4). Removals in this study were slightly lower than those reported for single visits by *Apis* on other varieties of apple (mean 69%, nectar visit 52%, pollen visit 86%; Freitas 1995), but we quantified the available pollen differently. Removal rates in our study fell within the range of published data for single bee visits to other plants (Snow & Roubik 1987; Thomson & Thomson 1989; Wolfe & Barrett 1989; Young & Stanton 1990; Wilson & Thomson 1991).

Sideworking *Apis* made less contact with the sexual parts of flowers, reducing removal and deposition. *Apis* adopted sideworking behaviour on 20–30% of the nectar-collecting visits to Delicious varieties, but at much lower rates on other varieties (Fig. 2). Benedek & Nyéki (1996) found frequencies of sideworking of up to 66% of *Apis* visits on certain varieties, which suggests that the behavioural differences between *Apis* and *Bombus* may be even greater on other varieties. On Rome flowers, *Apis* removed a smaller proportion of pollen grains while making frontal nectar visits than while making pollen-collecting visits. Therefore, the proportion of nectar- vs. pollen-collecting visits made by *Apis* will influence pollen-transfer dynamics.

Surprisingly, *Bombus* removed similar amounts of pollen during nectar visits and pollen visits. Because we estimated pollen removal from the amount of pollen remaining in the anthers after a visit, we do not know how much of the removed pollen actually stayed on the bee in exposed sites from which it could be transferred to stigmas. Pollen grooming by apid bees, whether into corbiculae or off the body entirely, wastes so much pollen that less than 1% is likely to reach stigmas (Thomson & Thomson 1989; Stanton *et al*. 1992; Holsinger & Thomson 1994). Rademaker, De Jong, & Klinkhamer (1997) estimated that 50% of the pollen removed during a *Bombus* visit to *Echium vulgare* is lost from both the flower and the bee, even before the bee arrives at the next flower. We do not know how the reward sought by the bee influences the proportion of pollen wasted, although some data suggest that bees adjust the frequency and duration of grooming efforts depending on pollen availability (Harder 1990). Pollen collectors may actually circulate a smaller proportion of the pollen they remove than nectar collectors (theoretically considered by Harder & Wilson 1997, 1998).

Bombus deposited more pollen onto apple stigmas than *Apis* (Fig. 5). On Rome, this difference primarily reflected greater deposition by *Bombus* during pollen-collecting visits. On Golden Delicious, it reflected low deposition by sideworking *Apis* compared with frontal nectar visitors of either *Bombus* or *Apis*. On Golden Delicious, however, *Bombus* nectar visits deposited slightly more pollen than *Apis* visits of any type (Fig. 5b). We could not obtain enough pollen-collecting visits for either bee for analysis, because such bees avoided emasculated flowers. Differences among bees in deposition might reflect differences in bee size if *Bombus*' larger surface area allows more contact with the stigmas. Thomson (1986) found that larger *Bombus* queens made more contact with *Erythronium grandiflorum* stigmas. Similarly, larger bees deposited more pollen on *Cassia* flowers than smaller bees (Snow & Roubik 1987). Although deposition may increase with body size within apid bees, Kendall & Solomon (1973) found that smaller andrenid bees carried more apple pollen on their bodies than *Apis* or *Bombus* (not including corbicular loads), suggesting that these smaller bees could potentially deposit as much or more than the larger species.

Almonds

On almonds, Bombus removed only slightly more pollen than *Apis* (40% and 32%, respectively; Fig. 6). However, most of the visits were pollen-collecting visits, which may affect the results. *Apis* tended to remove less during nectar visits. *Apis* and *Bombus* deposited similar numbers of grains on almond stigmas (Fig. 7). The small stigma loads probably reflect the low availability of pollen in background forage in the tent, and should be viewed in a comparative context only, not assumed to reflect field values.

In contrast to the results from apples, bee behaviour did not significantly influence removal or deposition. Several factors may underlie this discrepancy. First, Mission almond flowers do not facilitate sideworking by honeybees (K. Goodell, personal observation). Unless they are sideworking, honeybees do not differ radically from bumblebees. If other almond varieties do provoke sideworking, *Apis–Bombus* differences might emerge. Secondly, if bee size affects deposition, the smaller size difference between *Apis* and *Bombus* workers on almond than that between *Apis* and *Bombus* queens on apples may have reduced the importance of bee type in pollen deposition in almonds. Finally, most bees visiting almonds in our cage actively collected pollen during visits, so sample sizes for nectar-only visits were small. We had low power to test differences among removal rates and deposition by bees while nectaring.

METHODOLOGICAL PROBLEMS

Although we advocate measurement of pollen removal and deposition for preliminary comparisons of pollinators, there are technical obstacles. Directly measuring removal is impossible because the available grains cannot be counted before the visit. Several researchers have estimated pollen removal by quantifying pollen transferred to the bee, pollen lost onto petals or into the air, in addition to the pollen remaining (Harder & Thomson 1989; Murcia 1990; Rademaker, De Jong, & Klinkhamer 1997), but these methods are not practical in all systems. The best systems for measuring pollen removal are ones that present a non-destructive and easily measured correlate of pollen availability, such as anther length in *Erythronium grandiflorum* (Thomson & Thomson 1989). In apples and almonds, the best estimator available to us came from averaging pollen counts from approximately half of the anthers in a flower. Bees should not have perceived these flowers as unnatural because the anthers typically dehisce gradually in the field (J. D. Thomson, personal observation). Unfortunately, pollen production per anther was variable enough that we occasionally obtained negative estimates of removal. Such inaccuracy inflated error variance and thereby reduced our ability to differentiate between *Apis* and *Bombus*. The removal rates we report fell within the ranges of removals estimated in other studies; differences in removal that we did detect were in the predicted directions. Therefore, although our protocol for bee comparisons has limited power, it is probably free of bias.

Quantifying deposition of pollen on stigmas is straightforward if self-pollen deposited on the stigma during the visit can fertilize ovules, i.e. if there is neither self-incompatibility nor inbreeding depression. Then, all grains can be counted. In the case of apples and almonds, self-pollen will not fertilize ovules. To count the number of out-crossed pollen grains deposited, one either has to emasculate flowers to avoid self-deposition or be able to distinguish the pollen grains visually. The latter is difficult (but see Thomson & Thomson 1989; DeGrandi-Hoffman *et al.* 1992). Therefore, although we could not eliminate geitonogamous grains, we emasculated recipients to avoid the large numbers of intrafloral self-grains that greatly hampered counting. Emasculation, however, may alter bees' behaviour. It can discourage bees from attempting pollen-collecting visits (K. Goodell, personal observation) and can also provoke abnormal posture while nectar collecting (Rademaker, de Jong & Klinkhamer 1997). On apples and almonds, bees were less likely to attempt active pollen collection on emasculated flowers, although occasionally they would scrabble at the severed tips of the stamens as if they were collecting pollen. We also obtained some deposition data from intact flowers that had no dehisced anthers. Bees visiting these flowers did not adopt unusual postures, and they sometimes attempted to collect pollen.

RECOMMENDATIONS FOR FURTHER STUDY AND FOR MANAGING POLLINATION

Clearly, the number of pollinators that can be induced to work a crop is the basic determinant of pollination sufficiency. Beyond the issue of numbers, three aspects of individual bees are most important to their overall effectiveness: the number of visits per unit time, the compatibility of the pollen delivered, and the quantitative balance between removal and delivery. We concentrated on the last of these, because our models showed that it could counteract the effects of numbers: a handful of high delivery (HD) pollinators can in principle deliver more pollen than an infinite number of low delivery (LD) pollinators. We found nothing so drastic. Although *Bombus* queens are better pollinators of apple than *Apis* workers, in the sense of delivering more grains relative to the amount they remove, the differences are modest. Furthermore, the differences are really marked only on apple varieties that provoke side-working by nectar-seeking honeybees. When *Apis* do sidework, they act as LRLD pollinators, not HRLD. Unlike HRLDs, LRLD pollinators are unlikely to interfere with the efforts of better pollinators.

Whether a LD species really becomes a functional parasite when paired with a HD species depends on many other factors. Some of these have been modelled in BeeVisit (Thomson & Thomson 1999), such as the presentation schedule of pollen in the anthers, the shapes of the delivery functions, and the rate at which pollen becomes inviable (Thomson & Thomson 1992, 1999). Others involve post-pollination processes, which can act in very elaborate ways. For example, our models simply assume that more grains arriving at stigmas means better pollination. In fact, the mathematical relationship between agriculturally important fruit or seed set and compatible pollen receipt is likely to be a non-linear saturating or sigmoid function. We found that even sideworking *Apis* usually deliver at least 100 pollen grains. This quantity may be more than enough to fertilize the 10 apple ovules if many of these grains are viable and compatible, with little advantage gained from more grains. Had *Bombus* and *Apis* differed more strikingly with respect to removal and delivery, we would have advocated further study of these additional factors. Given our findings, these questions seem less critical.

Not all delivered grains are compatible. In both apples and almonds, the necessity for intervarietal pollen transfer may mean that interactions among orchard geometry, bees' willingness to fly between trees and rows, and the probability of bee-to-bee transfer within the hive (Tufts & Philip 1922; DeGrandi-Hoffman, Hoopingarner & Baker 1984; DeGrandi-Hoffman, Hoopingarner & Klomparens 1986; Vezvaei & Jackson 1997) may influence yields more dramatically than the overall delivery efficiency that our models address. Kendall (1973) tested the viability and compatibility of pollen grains carried on the bodies of bee visitors to apples: *Apis* carried 20–50% viable apple pollen grains, similar to the proportion obtained from freshly dehisced anthers. The compatibility of those grains differed among bee species and depended on the spatial arrangement of varieties within the orchard. Kendall (1973) pollinated virgin apple stigmas with the bodies of anaesthetized bees caught while foraging naturally on apple flowers. Pollen from pollen-collecting, but not nectar-collecting, honeybees resulted in more ovules fertilized than self-pollinated controls. Furthermore, when he repeated this study in orchards with compatible pollenizers planted in alternating rows, rather than within rows, the bodies of neither pollen- nor nectar-collecting *Apis* resulted in significantly more ovules fertilized than controls. Unfortunately, the sample size for *Bombus* was too small to draw conclusions. Notably, however, *Andrena* outperformed *Apis* in the compatibility tests, even in orchards with the greatest distance between compatible trees. It would be interesting to compare pollen removal and deposition of *Andrena* spp. on apples with those of *Apis* and *Bombus*. Foraging speed of pollinators can also contribute to overall importance of different pollinator species. *Bombus* makes quicker visits to apple flowers, allowing them to visit more flowers per unit time (Table 1; Shaw, Bailey & Bourne 1939). These aspects of behaviour deserve more study.

Apis cost far less per forager than *Bombus* (Dogterom 1999). Therefore, although apple growers would be well advised to manage their orchards to encourage natural populations of *Bombus*, a superior pollinator per visit, our work does not provide much reason to replace *Apis* hives with bumblebee colonies. Based on pollen depletion alone, bumblebees may be worse pollinators of almond than honeybees because they appear to remove slightly more relative to the amount they deposit than do honeybees. If bumblebees have any advantages in almonds, they would be attributable to working speed, movement patterns, ability to fly in cool spring weather, or some other aspects not related to per-visit pollen-transfer efficiency.

Our work does yield some recommendations for management. Pollen-collecting *Apis* deposited more on apple stigmas than nectar collectors, especially on Delicious. *Apis* colonies flexibly allocate workers to collecting pollen or nectar depending on the state of the colony (Fewell & Winston 1992; Seeley 1995). Managing hives for maximum pollen collection (Thorp 1996), especially when Delicious varieties comprise all or part of the orchard, would increase deposition per visit. In almonds, management of both honey and bumblebees for nectar collection may maximize the delivery of grains per number removed. *Bombus* also respond to deficits of stored pollen or nectar by increasing foraging effort allocated to collecting the limiting resource (Plowright *et al*. 1993, 1999). Commercial *Bombus* colonies are usually shipped with a large 'nectar' reservoir (designed to induce pollen-collecting on tomato flowers). Almond growers might get better service by removing this reservoir.

Pollen-collecting behaviour need not produce better pollination service for plants. It arises in apples primarily because nectar collecting and sideworking are linked. Without this connection (in varieties other than Delicious, for example), pollen collectors differ little from nectar collectors. In other plants, where active pollen collectors remove more pollen and deposit less (Wilson & Thomson 1991), pollen collectors may diminish total pollen transfer. Crops on which honeybees and native pollinators adopt different foraging behaviours, such as cashew (*Anacardium occidentale*; Freitas & Paxton 1998) and squash (*Cucurbita pepo*; Tepedino 1981), deserve particular study in this regard.

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