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Chapter 11

Comparing Pollinator Quality of Honey Bees (Hymenoptera: Apidae) and Native Bees Using Pollen Removal and Deposition Measures

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ABSTRACT *Relative pollinator quality can be measured in terms of the amount of pollen removed from anthers and subsequently deposited on stigmas, combined with the rate of floral visitation. Most studies compare crop pollinators on the basis of seed yield or pollen deposition. Considering pollen removal may give additional insight into pollinator quality, particularly in systems where pollination is limited by insufficient pollen transfer. Using a pollen removal–deposition measure, we compared three native bees and honey bees (*Apis mellifera *L.) visiting the native annual* Phacelia tanacetifolia *Benthem. Honey bees removed significantly less pollen per visit than any native pollinator. Bumble bees (*Bombus *spp. Latreille) and* Anthophora urbana *Cresson deposited relatively more pollen on stigmas than either honey bees or* Osmia lignaria *Cresson. Per-flower visitation rates also differed among bees.* A. urbana *were at least three times faster than any other species. According to a pollen removal and deposition measure of quality,* Bombus *spp. and* A. urbana *are relatively good* P. tanacetifolia *pollinators. Honey bees are poorer because they move little pollen into circulation.* O. lignaria *are the worst because they deposit little on stigmas and may remove pollen from the system that could be deposited by other species. A removal and deposition*

perspective cannot be substituted for comprehensive study of seed yield by different pollinators. However, the removal and deposition method, combined with pollen transfer models, may provide a powerful complement to explore systems with multiple visitors and screen candidate pollinators in conjunction with studies of pollinator biology.

Despite differences in the quality of pollination provided by different pollinators, managed pollination of native and introduced crop species has relied primarily on a single species, the honey bee, *Apis mellifera* L. The honey bee's unique advantages with regard to numbers and manageability make it a dominant pollinator in most agricultural systems. Even in situations where it does not work flowers efficiently, a manager can import huge numbers in an attempt to "saturate" pollination (Robinson et al. 1989). On certain crops, however, honey bees' flower-visiting preferences and behavior seem to preclude the advantages of number, producing occasional or even chronic pollination deficits (e.g., Sampson et al. 1995, MacKenzie and Javorek 1996). For some crops—alfalfa, greenhouse tomatoes, fruit trees—native or alternative introduced pollinators have been successfully managed or have supplanted honey bees (Stephen 1959, Maeta 1990, Banda and Paxton 1991, Peterson et al. 1992, Richards and Meyers 1996).

These successes make powerful arguments for continued investigation of alternative pollinators, particularly native bees, to exploit the variation in pollinator quality more fully (Parker 1981, 1982; Cane et al. 1996). Even where honey bees currently are considered adequate, supplementation or substitution with alternative species may improve pollination (Torchio 1985, Bosch and Kemp 1999). Unfortunately, developing an alternative pollinator requires long, comprehensive study of the candidate species' biology and management. We propose that a quick assessment of pollen removal and delivery rates can be used to screen candidate taxa, so that development efforts can be concentrated where success is most likely.

What makes a good pollinator? Evolutionary ecologists define pollinator quality in terms of fitness through female and male plant function (Stanton et al. 1991). Pollinator differences that affect fitness must act through patterns of pollen removal and delivery (Campbell et al. 1996, Wilson and Thomson 1996). One way to understand differences in pollinator quality is to measure pollen removal (from anthers) and deposition (on stigmas) during visits to individual flowers (Young and Stanton 1990, Wilson and Thomson 1991, Conner et al. 1995, Goodell and Thomson 1996, Freitas and Paxton 1998). Although removal and deposition data must be interpreted carefully (Harder and Barrett 1996, Waser 1988, Thomson and Thomson 1989), they usually have some relationship to plant fitness (Young and Stanton 1990, Ashman 1998, but see Harder and Thomson 1989). As Wilson and Thomson (1996) point out, "If neither removal nor deposition were related to pollination variation, it is hard to imagine how fitness could be." When combined with measures of visitation rate, removal and deposition can provide a first approximation of a pollinator's contribution to plants' reproductive success through female and male function.

In contrast, agriculturally oriented comparisons of different pollinators understandably focus on female function, especially as it is reflected by yield-related measures such as the total, or per-visit, fruit or seed yield produced by single pollinator species. Some studies have measured pollen deposition (Cane et al. 1996, Stubbs and Drummond 1996). All else being equal, high-deposition visitors are assumed to be "good" because more grains per stigma should translate to higher yield; that is, deposition is measured primarily as a proxy of yield, which also gives insight into the mechanism by which different visitors confer different yields.

Pollen removal has received much less attention because paternity usually is considered of little consequence to yield except in special cases such as hybrid production. We argue that pollen removal deserves more study because recent work has shown how effectively some visitors remove pollen from anthers (Wolfe and Barrett 1987, Wilson and Thomson 1991, Corner et al 1995, Thomson and Goodell 2001). In agricultural systems, as in natural populations, the supply of pollen ultimately may limit pollination.

When pollen supplies potentially can be depleted, pollinator quality depends on the interplay of removal and deposition. This dependence has been investigated by mathematical pollen–depletion models (Harder and Thomson 1989, Thomson and Thomson 1992). There are three key variables: the amount of pollen removed from anthers, the proportion of the removed pollen that is subsequently deposited on stigmas (transfer efficiency), and the visitation rate.

Deposition and removal must be considered together because their balance determines how overall pollen delivery varies with visitation rate. A pollinator with a high removal rate (HR) will perform the necessary task of getting pollen out of the anthers. With a high deposition rate (HD), the pollinator also effectively delivers pollen. If instead, the pollinator has a low deposition rate (LD), most removed pollen is lost from the system. A pollinator that removes little pollen per visit (LR) but delivers it effectively (HD) may be far better *if* its visitation rate is high enough, but may be worse if it visits so infrequently that most pollen never leaves the anthers.

The situation becomes more complex when multiple visitors that have different removal–deposition patterns are considered within a system (Wilson and Thomson 1991, Thomson and Thomson 1992). HR–LD species, by removing from circulation pollen that otherwise would have been delivered by other species, can prevent those other species from doing a good job and actually reduce pollen delivery by their presence. Furthermore, because the negative effects of HR–LD species come about through excess depletion of pollen, the tactic of increasing bee numbers to "saturate" the crop would be counterproductive.

Are there general characters that make good pollinators? In view of the preceding review of pollen–depletion models, we consider two related generalizations about the relative values of different pollinators:

1) Pollen-collecting bees are better pollinators than nectar-collecting bees.
2) Bee species specialized on the plant are better pollinators than more generalized species.

We argue that neither statement can be accepted as generally true.

On certain crops, some individual bees specialize on active pollen collecting, whereas others of the same species concentrate on nectar. Free (1970) suggested that the former should be better pollinators. Pollen collectors must contact stamens and may touch stigmas in the process. Free's proposition is reasonable when considering broad differences in behavior such as sideworking of flowers (Roberts 1945, Remacle 1989, Robinson et al. 1989, Goodell and Thomson 1996) or the special case of flowers with poricidal anthers that require active pollen extraction to move pollen into circulation (e.g., Buchmann 1983). For species with imperfect or protandrous flowers, the value of pollen foragers can be reversed if the foragers do not visit female flowers often (Tepedino 1981, Wilson and Thomson 1991). Even with cosexual flowers, pollen collectors actively groom pollen into scopae or corbiculae after a flower visit, so they might deposit less of it on receptive stigmas.

Several authors have suggested that specialist visitors (typically solitary bees) are likely to be better pollinators than generalists (e.g., Tepedino 1981, Parker and Frohlich 1983). Specialist visitors are likely to be timed with flower bloom (Tepedino 1981, Minckley et al. 1994) and may remain more flower constant (sensu Waser 1986), thereby minimizing heterospecific pollination and pollen waste. Additionally, it is supposed that pollinator and plant have coevolved to some degree, so the bee is likely to be more efficient in pollen transfer.

As Tepedino (1981) points out, the coevolution argument is unconvincing; pollen transfer efficiency requires empirical investigation (also see Schemske 1983, Thompson 1994). Although specialists are likely to be efficient pollen removers (HR; Strickler 1979), there is no reason why a specialist should *deposit* pollen well (HD). Indeed, if specialized bees have scopae that are particularly adapted for holding the pollen of their specialty, they may tend to be HR–LD bees. The relationship of specialization and pollinator quality deserves further testing.

Comparing pollinators with pollen transfer parameters. Rather than considering pollination effectiveness, strategies for investigating candidate pollinators have begun with extensive work on nesting, foraging biology, and pollinator management (Torchio 1990, 2003), culminating in large-scale field trials that measure seed set resulting from visitation by single pollinators (but see Cane et al. 1996). This long and costly process tends to be completely empirical. To the extent that "theory" enters at all, it probably enters in the form of generalizations of the sort that we have questioned in the preceding sections. Ultimately there is no substitute for direct assessment of pollination and seed/fruit yield in field trials. However, much effort might be saved by some prescreening of pollinator quality based on pollen removal and deposition parameters combined with pollen–depletion models. This might help focus efforts on fewer pollinator species for the crop of interest. To illustrate the approach, we present data from a comparative study of four bee species covisiting the same plant. We restrict the scope of this chapter to comparing removal and deposition rates, considering models elsewhere (Thomson and Thomson 1992, Wilson and Thomson 1996, Thomson and Goodell, 2001).

We took advantage of populations of *Phacelia tanacetifolia* Bentham (Hydrophyllaceae) growing in agricultural land in Cache Valley, Utah, to compare pollinator pollen removal and deposition across four dominant visitors: *Apis mellifera* L. (Apidae: Apini), *Bombus* spp. Latreille (Apidae: Bombini), *Anthophora urbana* Cresson (Apidae: Anthophorini), and *Osmia lignaria* Cresson (Megachilidae: Osmiini). In this chapter, we consider whether quality is correlated with pollen versus nectar foraging and foraging specialization and note how differences in morphology and foraging behavior affect single-visit pollinator efficiency. We then discuss how combinations of different visitors might interact to affect overall pollination.

Materials and Methods

Study System. *Phacelia tanacetifolia* is a California native annual that blooms from late spring to midsummer. Flowers are borne on one or more three-fingered cymes that uncoil as flowers open. New flowers open throughout the day so that inflorescences have several open flowers in various stages at the same time (Williams 1997). Flowers appear to be protandrous and are reported to be self-compatible (Knuth 1909). Each fruit produces four small nutlets. Anthers dehisce synchronously and fully within 2 hours after the petals begin to unfurl. The long paired styles uncurl at the same time, but remain reflexed beyond the ring of anthers throughout most of the first day so that the tiny stigmas are considerably beyond the anthers. Stigmas appear unreceptive on the first day (unpublished data). Over the last part of the first day and throughout the second, the styles elongate and come together so that the stigmas are within the ring of anthers. Nectar is produced continuously throughout the two days, reaching a volume of 0.77 ± 0.15 µl (SD) per flower (also see Williams 1997).

Phacelia is not a traditional agricultural crop, but it is being investigated in the United States and Great Britain as an intercropping species. Its high nectar and pollen production, combined with profuse and prolonged blooming, make it a good candidate for sustaining bee pollinators during times when the crop of interest is not blooming. Intercropping to maintain pollinators may be increasingly important as natural plant populations are disrupted for agricultural and suburban growth (Williams and Christian 1991, Corbet 1995).

Flower Visits. We collected pollen removal and deposition data during the last week of June and first week of July 1995 and 1996. Data were collected for one set of flowers on the same day that they opened (first-day flowers) and a second set on the day after they had opened (second-day flowers). All plants from which we sampled flowers were housed in a large flight cage, free of flying insects. First-day flowers were marked on the morning of their use between 900 and 1000 hours. Second-day flowers were marked between 1400 and 1600 hours, the day before measurements were to be made.

Visit protocols, conducted between 1200 and 1500 hours, were identical for all bee species. Immediately before a trial, a single anther from the test flower was removed and placed in ethanol. The inflorescence containing a marked flower then was removed from the plant, placed at the end of a long stick, and offered to a bee foraging in the uncaged stand of *P. tanacetifolia* (Thomson 1981). We classified each visit as a nectar, pollen, or nectar–pollen visit. Following the visit, the four remaining anthers were removed and placed in a separate vial, taking care to avoid dislodging the residual pollen. We mounted the stigmas in molten, fuchsin-tinted glycerin jelly on microscope slides.

We scored flower-visit duration for each visitor species in a large *P. tanacetifolia* field near the experimental array. Visits were monitored between 1200 and 1400 hours on two days during peak bloom. We used visit duration to estimate the rate of flower visitation for different bee species. Interfloral flight durations were not quantified exactly, but these appeared to correlate with flower-visit duration (e.g., *Anthophora urbana* made rapid visits and also flew most rapidly among flowers).

Scoring Removal and Deposition. We counted the number of grains in the unvisited anther and the number remaining in visited anthers using an Elzone 280-PC particle counter (Particle Data, Elmhurst, IL). We estimated the number of grains removed per anther per visit by subtracting the number of grains remaining in a visited anther (mean of the four anthers) from the number in the unvisited anther for that flower. We counted the number of grains deposited on the stigmas with a compound microscope. We compared the proportion of grains removed using 2-way ANOVA followed by paired comparisons of all bees (Tukey LSD; Sokal and Rohlf 1995). Data were arcsine-transformed before analysis. Pollen deposition was compared using nonparametic tests (Kruskal–Wallis test followed by Mann–Whitney U tests with Bonferroni adjustment; Sokal and Rohlf 1995). We report analysis only for second-day flowers for which stigmas are receptive.

The proportion of removed pollen that is deposited on visits to single flowers gives a first approximation of transfer efficiency. We calculated two measures of efficiency for each bee species. First, we estimated "paired-count efficiency" based on paired counts of deposition and removal within single visits. First-day flowers are not yet receptive (unpublished data), therefore we used only second-day transfer data for this first index. Second, we estimated "two-day efficiency" as the average number of grains deposited on second-day flowers divided by the average number of grains removed on first-day flowers. The two-day measure recognizes that, under reasonably high visitation rates, pollen typically may be available only on the first day, but stigmas are receptive only on the second day. Because we cannot pair the data for

removal and deposition for single visits, we report two-day efficiencies as bee-species averages only, with no estimates of standard error.

Results and Discussion

Comparisons among Bee Species. Pollen removal and deposition differed among bees and between first- and second-day flowers. All bees removed a greater proportion of pollen from second-day flowers than from first-day flowers (Fig. 1; Table 1). Honey bees removed a significantly lower proportion of available pollen than any of the native bees, which did not differ from each other (Fig. 1). Deposition patterns differed from removal. Bumble bees and *A. urbana* deposited more grains (12 and 11 median per visit; Fig. 2) than honey bees or *O. lignaria* (3 and 2 median per visit) during visits to second-day flowers. Even if all deposited grains lead to viable seeds, on most visits honey

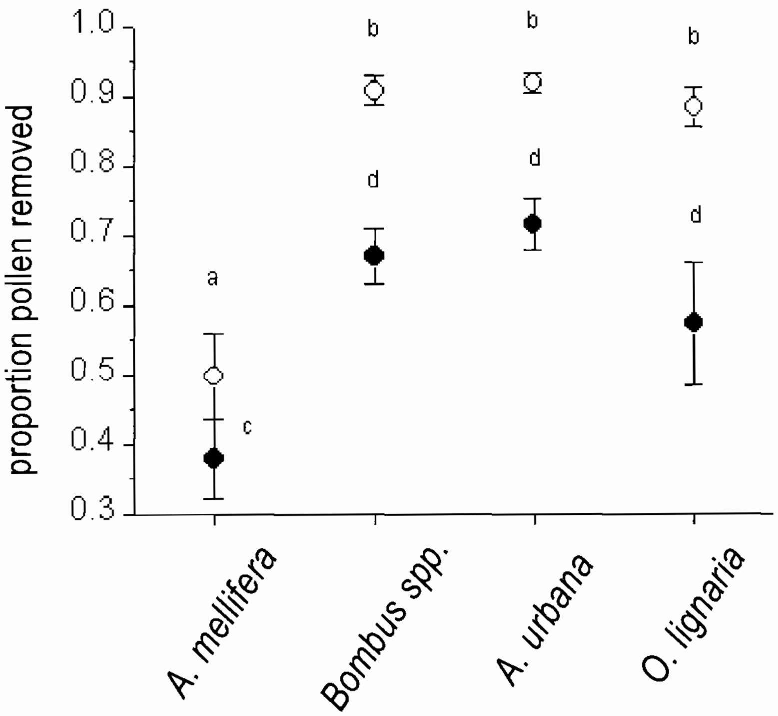

Fig. 1. Proportion of pollen removed (mean ± std. error) by each bee species during single visits to individual flowers. ● = first-day flowers, ○ = second-day flowers. Sample sizes for first-day flowers: *Apis mellifera*, 18; *Bombus* spp., 19; *Anthophora urbana*, 9; *Osmia lignaria*, 29. Second-day flowers, *Apis mellifera*, 31; *Bombus* spp., 37; *Anthophora urbana*, 33; *Osmia lignaria*, 35. Different letters indicate significant differences (Tukey LSD).

Table 1. ANOVA results for pollen removal by four bee species visiting first- and second-day flowers of *Phacelia tanacetifolia*

Source	df	Type III SS	F	*P*
Bee species	3	5.87	33.84	<0.001
Flower age	1	3.45	59.58	<0.001
Bee species × flower age	3	0.32	1.85	0.140

bees and *O. lignaria* do not deposit enough grains to achieve full seed set (honey bees 19 of 31 and *O. lignaria* 21 of 35 visits deposited <4 grains). All bees deposited similarly few grains on first-day flowers (median for *Bombus* spp. = 1, all other species median = 0).

We characterized bumble bees and *A. urbana* as HR–HD, honey bees as LR–LD, and *O. lignaria* as HR–LD. Paired-count pollen transfer efficiency (grains deposited/grains removed) also differed among pollinators. *O. lignaria* was significantly less efficient than bumble bees and *A. urbana*, but did not differ from honey bees (Table 2). Honey bees also were significantly less efficient than bumble bees. The two-day efficiency of *A. urbana* exceeded that of other bees (Table 2).

Comparisons among Visit Types within Bees. No consistent patterns of removal and deposition during pollen, nectar, and nectar–pollen visits to second-day flowers emerged among bees (Table 3). Instead, differences in each component of pollen transfer appeared to be related to unique behavioral and morphological characteristics of each bee species and behavior of individual bees. Some individuals of each species collected only pollen, others pollen and nectar during visits to single flowers.

Only some honey bees appeared to make exclusively "nectaring" visits. Perhaps in consequence, only honey bees showed substantial differences in pollen removal and deposition during visits of different types (Table 3). The quality of honey bees as *P. tanacetifolia* pollinators will depend greatly on the proportion of pollen versus nectar foraging individuals. Honey bees' nectar visits, which were more common than pollen visits, removed and deposited comparatively few grains (Table 3). Nectar-foraging honey bees typically arrived at the flower from the side, generally below the anthers. They worked their way in between filaments and so probed for nectar without actively contacting the anthers or stigmas of second-day flowers. During pollen visits, they approached and landed on the face of the flower and contacted anthers and stigmas.

Body position and behavior probably affected pollen transfer by bumble bees and *O. lignaria* as well. Bumble bees transferred somewhat more pollen during nectar–pollen visits than during pollen-only visits. They may have contacted anthers and stigmas more extensively while taking nectar because they probed more deeply into the flower and so pressed their thoraces against anthers and stigmas. We lack data on visit duration and so can not address its effect on pollen removal.

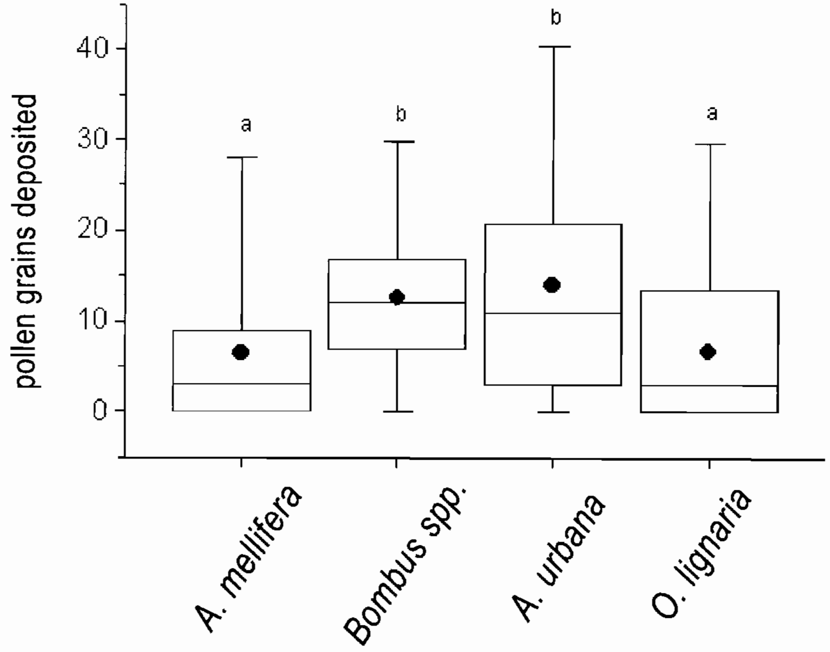

Fig. 2. Box plots of pollen deposition during single visits to second-day flowers of *Phacelia tanacetifolia* by each pollinator species. ● = mean, box gives quartiles and bars indicate range. Sample sizes: *Apis mellifera*, 31; *Bombus* spp., 37; *Anthophora urbana*, 33; *Osmia lignaria*, 35. Different letters above boxes indicate significant differences (Mann–Whitney U-Test Bonferroni adjusted *P* = 0.008 for multiple tests).

For *O. lignaria*, the pattern of pollen removal was reversed. *O. lignaria* made more contact with anthers and stigmas during active pollen visits than during nectar–pollen visits (Table 3).

On pollen-foraging visits, *A. urbana* often did not land, but instead stripped pollen with their outstretched legs. During nectar–pollen visits, in contrast, they landed to probe the nectaries, but neither deposition nor removal differed significantly between visit types.

Pollen Transfer and Specialist Bees. One particularly striking result was for *O. lignaria*. Although not considered an oligolege, it comes closer to being a *Phacelia* specialist than any of the other species. In natural populations throughout the western United States, females provision offspring predominately with pollen of Hydrophyllaceae (especially *Phacelia* and *Hydrophyllum*), *Salix*, and *Purshia* (Rust 1990; NMW, unpublished data). Rust (1990) suggested that *O. lignaria* favors flowers with exserted anthers and open corollas.

Table 2. Pollen transfer efficiency for four bee species to single flowers of *Phacelia tanacetifolia*

Bee species	% Efficiency "Paired count" median efficiency (upper & lower quartiles)^a	2nd-day mean deposition/ removal^b	"Two day" mean efficiency^c
A. mellifera	0.023 (0.0–0.07)b	0.053	0.014
Bombus spp.	0.087 (0.05–0.09)a	0.089	0.015
A. urbana	0.089 (0.013–0.15)a	0.106	0.102
O. lignaria	0.009 (0.0–0.058)b	0.032	0.014

Different letters indicate significant differences between species using Mann-Whitney U tests with Bonferroni adjustment $P = 0.008$, paired-count only.

[a] Deposition divided by removal, paired within flower visits. Data are for second-day flowers only.

[b] 2nd-day deposition divided by removal calculated as mean for each species rather than paired per visit.

[c] Average 2nd-day pollen deposition divided by 1st-day removal across all flower visits for each bee species.

During our study on *P. tanacetifolia*, a pollen-collecting female would tilt her body to be parallel to the filaments, her abdomen curled slightly over the anthers. She would then grasp stamens and carpels with her legs as she worked pollen into the metasomal scopa by brushing it over the anthers. Although the behavior accomplished extensive pollen removal, quite surprisingly the vigorous contact with anthers and stigmas did not deposit large numbers of pollen grains.

It is tempting to speculate that *O. lignaria*'s morphology, behavior, or perhaps electrostatics may be particularly adapted to retain pollen gleaned from this type of anther. Much of the pollen was removed directly to scopal hairs, which hold pollen grains during collection and transport to the nest. It makes sense that oligoleges in general will be specialized primarily for pollen collection and *retention*. Such adaptations would tend to reduce transfer efficiency, as they seem to do in *O. lignaria* visiting *P. tanacetifolia*.

It is worth noting that more comprehensive studies of *O. lignaria* as a pollinator of several orchard crops have shown it to be a superior pollinator (Torchio 1985). We do not see the differences as incompatible. The pollen removal–deposition method is plant species-dependent, so extending our data beyond *P. tanacetifolia* could be misleading. Careful observation of *O. lignaria* foraging on orchard crops might provide insight into differences in the results of the two studies. In addition, pollen removal and deposition measure pollinator quality in relative terms. *O. lignaria* may still effect seed set; we suggest only that relative to HR–HD visitors, it is a less efficient pollinator on *P. tanacetifolia*. The different results call for more investigation of pollinator quality from different perspectives, particularly in the case of more specialized visitors.

Combining Removal–Deposition Rates with Visit Speed to Compare Pollinator Quality. Bumble bees and *A. urbana* (both HR–HD) are relatively good pollinators of *P. tanacetifolia*, but *A. urbana* foraged more than three times faster (average of pollen and nectar–pollen visits, Table 3). Given its faster foraging, *A. urbana* would be a superior pollinator because fewer bees would be required to pollinate the same number of flowers. This ranking also would depend on the length of the foraging day for each species and the proportion of time spent foraging on other plant species, hence the total number of *P. tanacetifolia* flowers processed per individual.

Honey bees (LR–LD) did not set as much pollen in motion, were less efficient at transferring it, and worked more slowly than either bumble bees or *A. urbana*. When foraging for nectar, they were relatively poor pollinators of *P. tanacetifolia*. They would not deplete pollen from the system as rapidly as *O. lignaria* does, however, and therefore they would have different effects on the ability of other, co-visiting species to deliver pollen. By removing more pollen from the system (i.e., pollen that otherwise might have been delivered by other bees), *O. lignaria* is more likely to sabotage the pollinating potential of better visitors. Ranking these four species by the probable net value to *P. tanacetifolia* on the basis of single pollen transfer, we would predict *A. urbana* to be the best, followed by *Bombus* spp., then *Apis mellifera*, and finally *Osmia lignaria*.

Limitations of the Study and of the Method. Our conclusions are limited because of the practical difficulties of gathering certain kinds of data. Because similar problems are likely to crop up in other applications of our approach, we discuss them here to stimulate more thought on solving them.

First, we were unable to coax bees to visit emasculated flowers in a normal manner; therefore, we recorded deposition on intact flowers. Consequently, our deposition values include self grains from the test flower itself, in addition to xenogamous and geitonogamous grains imported by the bee. *P. tanacetifolia* is self-compatible so deposition may translate well into seed set. Given that self and geitonogamous pollen often have lower competitive ability, our estimates are likely upper bounds for effective deposition.

Second, the temporal separation of male function (mostly on day 1) and female function (day 2) complicated our attempts to measure removal and deposition in realistic ways. We measured pollen removal from second-day flowers that had not been visited previously. These flowers were rich in pollen, but second-day flowers in heavily visited agricultural or natural populations probably have lost most of their pollen. Our "two-day efficiency" measure is an attempt to take this protandry into account, but it entails a sacrifice of statistical testing.

Third, to model the full interplay of deposition and removal, we need to be able to specify the amount of pollen delivered from one focal flower to other flowers, as a function of the amount removed from the focal flower. If this function is nonlinear, as seems likely (Thomson and Thomson 1989, Harder 1990), then single-flower measures of removal and deposition can only provide educated guesses about pollinator quality.

Table 3 Summary of pollen transfer for 2nd day flowers of *Phacelia tanacetifolia* with visitation behavioral data for four bee taxa

Visit Type	% Visits	Proportion grains removed (SD)	Mean deposition (SD)	Mean duration (SD; *n*)	Forager Position
Apis mellifera (*n* = 29)					
Pollen	17	96.7 (1.2)	15.3 (13.0)	1.28 (1.44; 15)	Light landing at front of flower; contact with anthers and stigma; pollen collected with legs
Nectar	83	35.4 (22.4)	3.0 (6.6)	5.85 (5.69, 10)	Landing to side of flower below anthers and stigma; no pollen collected
Bombus spp. (*n* = 36)					
Pollen	22	87.6 (16.4)	8.8 (7.1)	No data	Landing at front of flower; no probe; contact with anthers and stigma; pollen collected with legs and on ventral body surface
Nectar–pollen	78	91.8 (12.4)	13.3 (8.5)	3.03 (1.91; 14)	Landing at front of flower; probe; contact with anthers and stigma; pollen collected with legs and on ventral body surface
Anthophora urbana (*n* = 33)					
Pollen	54	93.3 (5.7)	11.7 (11.3)	0.59 (0.16; 11)	Often in flight at front of flower; contact anthers and stigma; pollen collected with legs
Nectar–pollen	46	90.4 (9.8)	17.1 (14.8)	1.21 (0.75; 59)	In flight, then landing at front of flower; probe; contact anthers and stigma; pollen collected with legs and on ventral thorax
Osmia lignaria (*n* = 26)					
Pollen	12	89.8 (3.7)	8.3 (4.7)	1.53 (1.74; 10)	Landing front of flower; no probe; contact with anthers and stigma; pollen collected with legs and scopal hairs
Nectar–pollen	88	88.1 (12.3)	6.7 (9.5)	6.72 (3.59; 53)	Landing front of flower; probe; contact with anthers and stigma; pollen collected with legs and scopal hairs

Pollen removal and deposition during pollen or nectar–pollen visits were significantly different only for *A. mellifera* (Mann–Whitney U tests $P < 0.001$ for removal, $P = 0.06$ for deposition). Note sample sizes for visit duration differ from those for pollen removal and deposition.

To specify this functional relationship, however, we need to measure pollen carryover sequences for donor flowers containing different amounts of pollen, in conjunction with measuring pollen removal from those same donors. Accurately measuring carryover is intrinsically hard even if easily scored pollen markers are available, and it is practically impossible if they are not. However, if proper markers can be developed, they can solve the first two problems as well. First, emasculating recipients is neither necessary nor desirable if pollen from a focal donor can be distinguished from self pollen on a recipient stigma. Second, one can measure carryover from focal flowers that have received discrete numbers of previous visits onto strings of recipients that also include flowers with a realistic prior-visit distribution. We conclude that pollen depletion models can be fully parameterized for particular field situations only after the discovery or development of a convenient pollen marker system. Although this limitation is frustrating, it does not make pollen–depletion models worthless. By analogy, a partially parameterized model of nutrient flows through an ecosystem may not be fully complete until those flows have been quantified by tracer studies carried out in many conditions, but the incomplete model may still make plausible predictions about the general behavior of the system.

Finally, we reiterate that the method will be plant species-dependent so that generalizing results from the *Phacelia* system to *Prunus*, for example, could be misleading. Our intention here is to provide an example of the method in a multiple pollinator system.

In natural and agricultural populations, plants are visited by combinations of pollinators (Hurd et al. 1980, Parker 1981, Tepedino 1981, Schemske and Horvitz 1984, Herrera 1987). Achieving the best pollination strategy for a crop species depends on understanding how different visitors interact in field settings. Simple measures of pollen removal and deposition give us a chance of predicting some aspects of those interactions. When considering novel pollinators for introduction, we should be mindful of two lessons from pollen transfer: First, the mathematical demonstration that introducing a HR-LD species to a system that already has pollinators actually may reduce the amount of pollen being delivered (Thomson and Thomson 1992). Second, the empirical result that the most specialized bee in the *Phacelia* system acted as a HR–LD pollinator. In considering insect introductions for biocontrol of pests, narrow host specialization usually is considered a strong advantage. In pollination relationships, we should not accept this generalization uncritically.

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