

VISITATION, EFFECTIVENESS, AND EFFICIENCY OF 15 GENERA OF VISITORS TO WILD RADISH, *RAPHANUS* *RAPHANISTRUM* (BRASSICACEAE)¹

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Plant–pollinator interactions are one of the most important and variable mutualisms in nature. Multiple pollinators often visit plants and can vary in visitation rates, pollen removal and deposition, and spatial and temporal distribution, altering plant reproduction and patterns of pollinator-mediated selection. Although some visitors may not be effective pollinators, pollinator effectiveness is rarely estimated directly as seed set resulting from a single visit by each taxon visiting generalist plants. For two years, effectiveness of visitors to wild radish, *Raphanus raphanistrum*, was quantified by counting seeds set and pollen grains removed as a result of a single visit. We calculated a pollinator's importance to plant reproduction as the product of visitation rate and single-visit seed set, and regressed pollinator body size on pollen-removal and on seed set effectiveness. Although pollinators differed in effectiveness and visitation rates, pollinator importance was primarily determined by visitation rates. In contrast to similar 2-yr studies, pollinator assemblage composition varied little, suggesting pollinator-mediated selection can be consistent across years for this generalist. Larger pollinators were more effective than smaller at effecting seed set, but body size was a poor predictor of pollen removal ability. Instead, pollen-removal effectiveness may be more influenced by foraging behavior than size.

Key words: Brassicaceae; effectiveness; efficiency; generalization; pollination; specialization; visitation.

Because most species of angiosperms rely at least in part on animals for reproduction, the interaction between plants and pollinators is one of the most pervasive mutualisms in the natural world. Plant-pollinator interactions are also extremely variable. Although we do not know the relative frequency of generalization in plant–pollination systems in nature (Waser et al., 1996; Johnson and Steiner, 2000; Vazquez and Aizen, 2003), the pollinating community visiting a plant is often quite diverse during a given year (Herrera, 1987; Fishbein and Venable, 1996; Olsen, 1997; Memmott, 1999; Kandori, 2002; Ivey et al., 2003). Pollinator communities may also vary in the relative abundance of each taxon visiting a plant (visitation rate) and in the effectiveness of each taxon at transferring pollen (pollen effectiveness), with some plant visitors not pollinating at all (Spears, 1983; Schemske and Horvitz, 1984; Armbruster et al., 1989; Fishbein and Venable, 1996). Finally, pollinators often have considerable spatial and temporal variation in their visitation rates to a single plant species (Herrera, 1988; Horvitz and Schemske, 1990; Traveset and Saez, 1997; Fenster and Dudash, 2001; Ivey et al., 2003). Thus, to understand plant reproduction and floral evolution in generalist plant species, a thorough understanding of each pollinator taxon's effectiveness, visitation rate, and variation in visitation rates over time is essential. When measuring the degree of generalization of a plant's pollinator assemblage, pollination biologists have long recognized the need to estimate

a relative importance value for each visiting taxon (Johnson and Steiner, 2000; Fenster et al., 2004), which incorporates both a pollinator's quantity (visitation rates) and quality (effectiveness) (Lindsey, 1984; Olsen, 1997). However, few studies have fully characterized the pollinator importance of the majority of visiting taxa. We define pollinator importance as the total number of seeds set by each pollinating taxon relative to the total number of seeds produced during the study (Kandori, 2002).

Pollination biologists estimate effectiveness using many different methods. For example, researchers have quantified effectiveness as the amount of removal and/or deposition of pollen (Herrera, 1987; Pettersson, 1991; Fishbein and Venable, 1996; Ivey et al., 2003), the pollen load on pollinators (Lindsey, 1984; Sugden, 1986; Talavera et al., 2001; Moeller, 2005), and the probability of contacting stigmas and anthers (Lindsey, 1984; Sugden, 1986; Armbruster, 1988). Seed set is rarely used in measuring effectiveness (but see Schemske and Horvitz, 1984; Thompson and Pellmyr, 1992; Olsen, 1997; Kandori, 2002; Wiggam and Ferguson, 2005), despite the fact that the more common estimates of pollinator effectiveness may not accurately predict a pollinator's contribution to plant reproduction (Wilson and Thomson, 1991; Fishbein and Venable, 1996). Combining estimates of pollen removal with pollen deposition effectiveness (or with seed set) can provide an estimate of pollinator efficiency, defined as the number of pollen grains deposited or seeds set per pollen grain removed (Galen and Stanton, 1989; Harder and Thomson, 1989; Young and Stanton, 1990; Conner et al., 1995).

Although several researchers have documented differences among pollinators in their effectiveness at setting seed, the reasons for such differences are not well understood. Results from a few studies have shown that insects foraging for pollen are often less efficient than those foraging for nectar (Wilson and Thomson, 1991; Conner et al., 1995). Differences in visit duration among pollinators have been implicated in influencing pollinator effectiveness, with visit duration being positively

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related to both pollinator efficiency and effectiveness (Fishbein and Venable, 1996; Ivey et al., 2003) and negatively related to effectiveness (Boyd, 2004). Morphological aspects of pollinators such as tongue length (Schemske and Horvitz, 1984) and body size (Kandori, 2002) can also contribute to differences in efficiency, although few studies have examined how morphological differences among pollinators influence their effectiveness.

In addition to differences in effectiveness among pollinators, the pollinator assemblage visiting a plant may vary temporally because environmental fluctuations lead to fluctuations in the population dynamics of pollinator species (Herrera, 1988; Fleming et al., 2001). Variation in visitation frequency can alter selection pressure on floral traits from year to year (Schemske and Horvitz, 1989), which can hinder the adaptation of floral traits to any one pollinator (Herrera, 1988; Pettersson, 1991). Furthermore, in models used to predict when plants may be expected to specialize for a subset of the pollinator assemblage, increased temporal variation in pollinator assemblages decreased the likelihood of specialization (Waser et al., 1996).

This study measures the relative importance of 15 genera of insect visitors to *Raphanus raphanistrum* L. (wild radish). For each visiting taxon, we determined the (1) relative visitation rates during two years; (2) pollinator effectiveness (using both number of seeds set and number of pollen grains removed during a single visit); (3) pollinator importance (the proportion of the total number of seeds set during the season by each pollinator); and (4) pollinator efficiency (the number of seeds produced per pollen grain removed). To begin to understand the mechanisms behind differences in pollinator effectiveness, we examined the relationship between pollinator body mass and effectiveness.

MATERIALS AND METHODS

Study system—*Raphanus raphanistrum* is a hermaphroditic, annual herb that is native to Europe but has subsequently become a naturalized and prevalent agricultural weed on six continents (Holm et al., 1997). It is self-incompatible (Sampson, 1964), relying entirely on insect pollinators for plant reproduction, and it is visited by many different pollinator genera that span three insect orders: Lepidoptera, Diptera, and Hymenoptera (Kay, 1978, 1982; Conner and Rush, 1996). Visitors range in size from small sweat bees (e.g., *Dialictus* and *Halictus*) and syrphid flies (e.g., *Toxomerus*) to much larger honeybees (*Apis mellifera*), bumblebees (*Bombus*), syrphid flies (*Eristalis*), and cabbage butterflies (*Pieris rapae*) (Conner and Rush, 1996). In *R. raphanistrum*, most small bees and all syrphid flies collect or feed only on pollen (Conner and Rush, 1996), butterflies feed solely on nectar, and large bees feed on both pollen and nectar (Rush et al., 1995). Like most members of the Brassicaceae, *R. raphanistrum* has tetradynamous stamens, with four long and two short stamens. Mean long and short filament lengths in one natural population grown in the greenhouse were 11.7 and 9.7 mm, respectively (Conner and Via, 1993). *Raphanus raphanistrum* flowers have seven ovules on average (Conner et al., 1996a).

Seed set effectiveness—In 2002, plants were grown in 15-cm pots in a pollinator-free greenhouse and transported in a covered vehicle to old fields lacking *R. raphanistrum* at the Kellogg Biological Station in Hickory Corners, Michigan. These old fields were surrounded by farm fields, the principal habitat of *R. raphanistrum* in North America, and thus were likely to contain pollinators similar to those pollinating naturalized populations. To attract pollinators and provide pollen for seed siring, a 5-m diameter circular array of 15 plants was placed in the field and exposed to pollinators for 5 min, while focal plants were left in the covered vehicle to prevent visitation. After 5 min, one unvisited focal plant was placed in the center of the array. As soon as a focal plant was placed in the field, it was continuously observed. After each visit to a flower on the focal plant, the pollinator was identified to at least the

genus level, and a numbered straw was placed over the pistil to prevent further visitation. This was repeated for up to 20 flowers per focal plant and for up to 10 focal plants per day for 40 d throughout most of the flowering season (June–September). At the end of each day, all plants were returned to the greenhouse, the straws were removed, and each flower was tagged with a unique code corresponding to the code recorded for that single visit. Flowers were allowed to set seed, all fruits were collected, and the total number of seeds produced per fruit was determined. A total of 1315 seeds were produced from 2314 single visits.

A one-way ANOVA was used to test for differences between orders and genera of pollinators of *R. raphanistrum* in the number of seeds set during a single visit. Pollinator importance for each pollinator genus was calculated as the proportion of the total number of seeds set in this experiment by each pollinator, which is equivalent to the product of the number of visits and per-visit seed production (Kandori, 2002).

Pollen removal effectiveness—In 2001, plants were grown in the greenhouse as described above, and unvisited plants were transported to the same old fields at the Kellogg Biological Station, one of which contained a large experimental population of *R. raphanistrum*. One plant was placed in the field at a time and continuously observed for visitation. After a pollinator visited a flower, anthers from three long and two short stamens were removed from the visited flower and from the nearest unvisited flower on the same stalk and placed in separate clean vials, one vial for the long stamen anthers and one for the short stamen anthers. The fourth long stamen was preserved for subsequent measurement in a different study. The identity of the pollinator was recorded to the genus level when possible. This was repeated over several flowers per plant on up to 15 plants per day for 44 d from June through October, providing a total of 470 single visits. Pollen grains were counted using a ZBI Coulter counter (Beckman Coulter, Fullerton, California, USA; for details, see Rush et al., 1995). The number of pollen grains removed from anthers was estimated as the difference between the number of grains on the unvisited anthers and the number of grains remaining on the visited anthers (Harder, 1990; Young and Stanton, 1990; Rush et al., 1995). Adjacent *R. raphanistrum* flowers have similar pollen counts: 75% of the variation in pollen number is between plants rather than within a plant (Rush et al., 1995). Because of the small sample sizes for each genus, pollinators were divided into five functional groups based on size and taxonomy: small bees (*Halictus*, *Dialictus*, *Augochlorella*, *Ceratina*, and *Colletes*), large bees (*Bombus* and *Apis*), Lepidoptera (*Thymelicus* and *Pieris*), larger syrphid flies (*Allograpta*, *Sphaerophoria*, *Syrphus*, *Syritta*, and *Eristalis*), and the small syrphid fly (*Toxomerus*) (Table 1). Genera within each group did not differ significantly for pollen removal. One-way ANOVA was used to test for differences in pollen removal at both the order and the group levels.

To determine if pollen removal is a good predictor of seed set effectiveness, we averaged seed set effectiveness for each of the five groups tested for pollen removal and regressed seed set on pollen removal. To estimate pollinator efficiency for each pollinator, we divided the average number of seeds set by the average number of pollen grains removed in single visit. Finally, to test whether body size predicts seed set effectiveness, we regressed both pollen removal and seed set effectiveness based on the five functional groups on body size and regressed seed set effectiveness at the genus level on body size. Two to five individuals per insect genus were weighed after being air dried for at least 6 months. Dry body mass was averaged over all weighed individuals. *Colletes* samples were lacking, so the genus was not included in the regression of body size on effectiveness.

Pollinator visitation across years—Visitation rates of pollinator taxa in 2001 were compared to visitation in 2002. Because some pollinators were not identified to the genus level in 2001, some taxa were grouped based on size, resulting in nine pollinator groups (Table 1). Taxa from 2002 were placed in these same nine groups, and Spearman's rank-sum correlation coefficients (r_s) of visitation in 2001 and 2002 were calculated. JMP version 5.0.1.2 (SAS, 2003) was used for all analyses.

RESULTS

Seed set effectiveness—In 2002, *R. raphanistrum* was visited by 15 different genera (Fig. 1). Although we were unable to identify all visitors to the species level, a survey of *R.*

TABLE 1. Mean body mass of *Raphanus raphanistrum* visitors (+1 SE) and grouping levels for each analysis. *N* = number of insects weighed for each genus. No individuals of *Colletes* were available for body mass measurements.

Genus	Order	Functional group for pollen removal comparison	Grouping for comparison among years	<i>N</i>	Body mass (mg)
<i>Halictus</i>	Hymenoptera	Small bee	Small bee	3	10.2 (1.5)
<i>Dialictus</i>	Hymenoptera	Small bee	Small bee	3	2.4 (0.4)
<i>Augochlorella</i>	Hymenoptera	Small bee	Small bee	3	5.2 (1.6)
<i>Ceratina</i>	Hymenoptera	Small bee	Small bee	3	4.0 (1.4)
<i>Colletes</i>	Hymenoptera	Small bee	Small bee	—	—
<i>Bombus</i>	Hymenoptera	Large bee	<i>Bombus</i>	3	41.0 (10.2)
<i>Apis</i>	Hymenoptera	Large bee	<i>Apis</i>	3	30.0 (2.3)
<i>Thymelicus</i>	Lepidoptera	Lepidoptera	<i>Thymelicus</i>	2	18.9 (6.7)
<i>Pieris</i>	Lepidoptera	Lepidoptera	<i>Pieris</i>	2	25.7 (12.8)
<i>Allograpta</i>	Diptera	Large syrphid fly	<i>Allograpta</i>	3	5.9 (0.6)
<i>Sphaerophoria</i>	Diptera	Large syrphid fly	Large syrphid fly	3	3.6 (1.0)
<i>Syrphus</i>	Diptera	Large syrphid fly	Large syrphid fly	3	8.7 (1.6)
<i>Syritta</i>	Diptera	Large syrphid fly	Large syrphid fly	3	3.4 (0.1)
<i>Eristalis</i>	Diptera	Large syrphid fly	<i>Eristalis</i>	5	40.8 (7.7)
<i>Toxomerus</i>	Diptera	<i>Toxomerus</i>	<i>Toxomerus</i>	3	1.2 (0.4)

raphanistrum pollinators in Illinois in 1993 and 1994 (J. K. Conner, unpublished data) and our own identifications during this study indicate that there were probably two species in the genus *Halictus*; 11 species in the genus *Dialictus*; two species

in the genus *Bombus*; one species in each of the genera *Augochlorella*, *Ceratina*, *Colletes*, *Apis*, *Thymelicus*, *Pieris*, *Allograpta*, *Sphaerophoria*, *Syrphus*, and *Syritta*; three species in the genus *Toxomerus*; and two species in the genus *Eristalis*. Species within each genus are similar in terms of their morphology and behavior and thus are not likely to differ greatly in efficiency. *Halictus*, *Dialictus*, and *Augochlorella* are in the family Halictidae; *Bombus*, *Ceratina*, and *Apis* are in the family Apidae; and *Colletes* is in the family Colletidae. *Thymelicus* is in the family Hesperidae, *Pieris* is in the family Pieridae, and all flies are in the family Syrphidae.

Sweat bees in the genus *Dialictus* were the most frequent visitors, followed by the syrphid flies *Toxomerus*, *Syritta*, and *Eristalis*. These four genera made 81% of all visits to *R. raphanistrum*, and each of the other 11 pollinator genera accounted for less than 5% of the visits (Fig. 1A). Visitors from 14 of the 15 genera were effective pollinators, with an average seed set greater than zero (Fig. 1B). *Allograpta* (*N* = 17 visits) was the only taxon that did not effect any seed set during the experiment. Of the 14 effective pollinators, seed set effectiveness varied by more than an order of magnitude, from an average of 0.10 seeds per visit (*Sphaerophoria*) to 1.66 seeds per visit (*Apis*) (Fig. 1B). Despite the significant differences in effectiveness, pollinator importance was determined primarily by differences in visitation rates (Fig. 1). There was no relationship between a pollinator's visitation frequency and its effectiveness ($r^2 = 0.04$, $P = 0.48$).

The three orders of pollinators (Hymenoptera, Lepidoptera, and Diptera) differed significantly in their seed set effectiveness (Fig. 2A), with hymenopteran visits resulting in significantly higher seed set than dipteran visits. Lepidopteran effectiveness was higher than for the other two orders but not significantly so because of the small sample size.

Pollen removal vs. seed set effectiveness—All five groups of pollinators removed pollen during a single visit, but pollinators did not differ in the number of pollen grains removed from short stamen anthers ($F = 0.47$, $P = 0.76$). Pollinators did differ in the number of grains removed from long stamen anthers (Fig 3A) and in the total number of pollen grains removed when long and short stamen anthers were combined ($F = 2.41$, $P = 0.05$). *Toxomerus* removed the least pollen, and small bees and large syrphid flies the most.

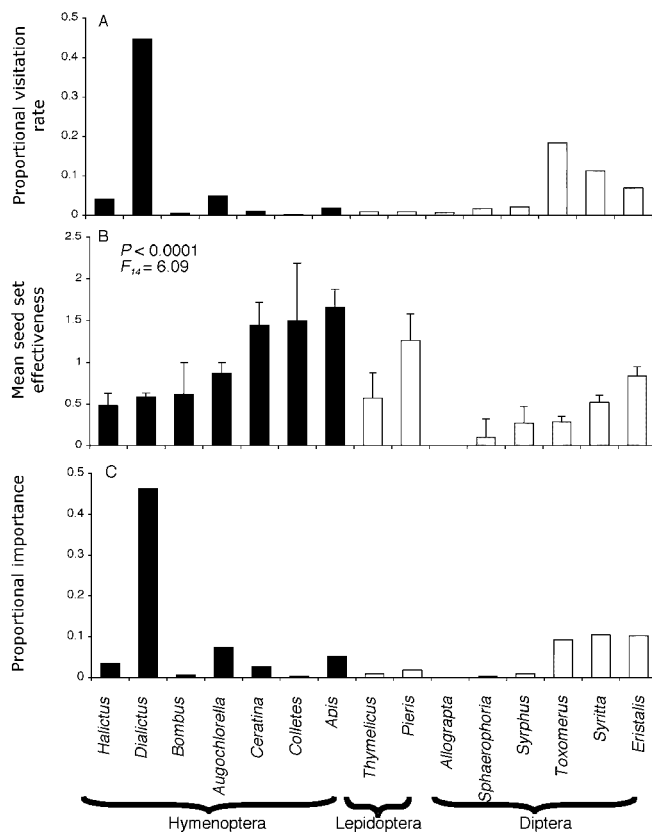


Fig. 1. (A) Visitation, (B) effectiveness, and (C) importance for each pollinator genus of *Raphanus raphanistrum*. Visitation is the proportion of total visits in 2002, effectiveness is the mean (+1 SE) number of seeds set during a single visit, and importance is the proportion of total number of seeds produced, equivalent to the product of visitation and effectiveness. Genera are grouped and shaded by insect order and arranged by increasing effectiveness within orders.

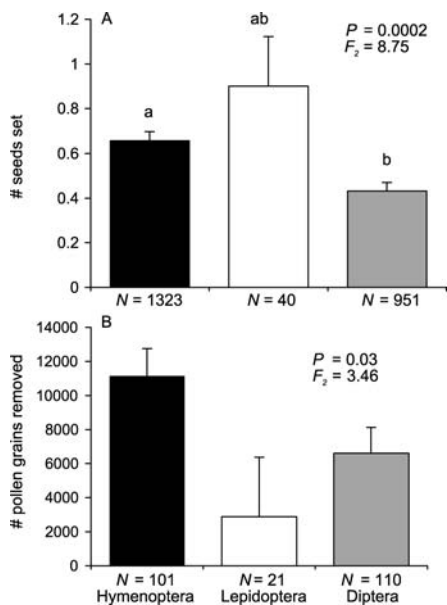


Fig. 2. Pollinator effectiveness of insect orders. (A) Seed set effectiveness and (B) pollen removal effectiveness for each order pollinating *Raphanus raphanistrum*. Seed set effectiveness is the mean (+1 SE) number of seeds set, and pollen removal effectiveness is the mean (+1 SE) number of pollen grains removed from long-stamen anthers during a single visit. Orders that do not share a letter in common are significantly different at $P \leq 0.05$ according to Tukey's HSD test. None of the pairwise differences were significant for (B).

Pollinators differed at the order level in pollen removal from long stamen anthers, with Hymenoptera removing the most, Diptera next, then Lepidoptera (Fig. 2B). When seed set effectiveness was analyzed using the same five pollinator groups, *Toxomerus* had the lowest seed set effectiveness, similar to its low pollen removal, but in contrast to the pollen removal results, small bees and large syrphid flies had low seed set effectiveness and large bees the highest (Fig. 3B). Thus, pollen removal effectiveness was not a good predictor of seed set effectiveness ($r^2 = 0.04$, $P = 0.76$).

Body size vs. effectiveness—Visitors to *R. raphanistrum* ranged in size by more than an order of magnitude, varying from 1.4 mg (*Toxomerus*) to 40 mg (*Bombus*) (Table 1). There was not a significant relationship between pollinator body mass and seed set effectiveness when all 15 pollinators were included in the analysis ($r^2 = 0.17$, $P = 0.15$). However, when one possible outlier, *Ceratina*, was removed from the analysis, there was a significant positive relationship between mass and effectiveness (Fig. 4A). *Ceratina* was also an outlier in terms of foraging only on nectar. Although this bee was similar in size to other halictids (Table 1), this foraging behavior was similar to that of the large honeybee *Apis* (H. Sahli, personal observation). When pollinators were grouped into the five categories used to analyze pollen-removal effectiveness, there was a strong relationship between body size and the number of seeds set during a single visit (Fig. 4B), but body size did not predict pollen removal (Fig. 4C).

Pollinator visitation rates—Visitation rates of different pollinator taxa did not differ temporally across 2001 and 2002

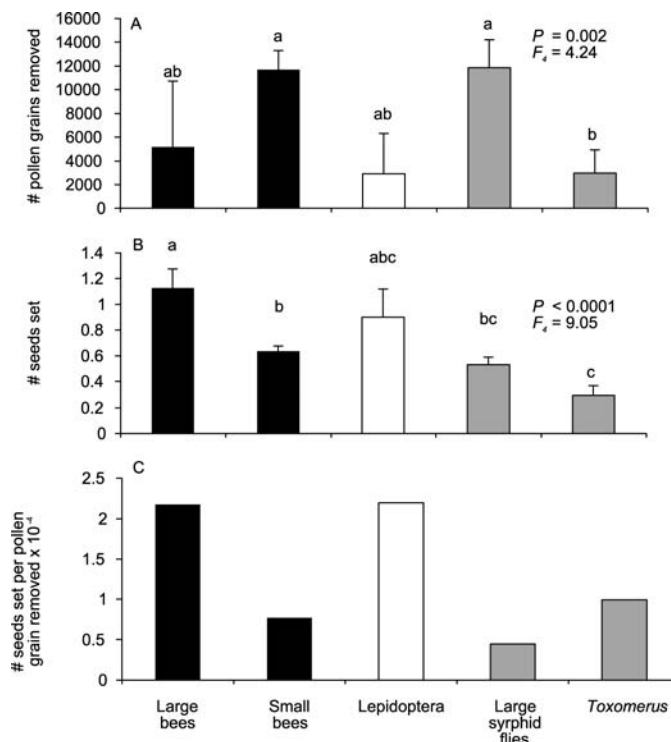


Fig. 3. Pollinator efficiency for five groups of pollinators. (A) Pollen removal effectiveness (number of pollen grains removed from long-stamen anthers during a single visit), (B) pollinator seed set effectiveness (number of seeds set during a single visit), and (C) pollen transfer efficiency. Because of small sample sizes for pollen removal effectiveness at the genus level, pollinators were placed into five groups. Large bees include *Bombus* and *Apis*; small bees include *Halictus*, *Dialictus*, *Augochlorella*, *Ceratina*, and *Colletes*; Lepidoptera include *Thymelicus* and *Pieris*; and large syrphid flies include *Allograpta*, *Sphaerophoria*, *Syrphus*, *Syrpita*, and *Eristalis*. Black bars are Hymenoptera, white bars are Lepidoptera, and gray bars are Diptera. Genera that do not share a letter in common are significantly different at $P \leq 0.05$ according to Tukey's HSD test.

(Table 2) because the visitation frequency for the nine pollinator groups was consistent across years ($r_s = 0.77$, $P = 0.01$). In both years, small bees were the most common visitor, followed by *Toxomerus* and medium syrphid flies. Because the majority (60%) of single visits in 2001 were made in a field adjacent to a large experimental population of wild radish, the similarity of visitation across years also indicates that visitors recorded in this study are likely to be representative of those in naturalized populations of wild radish in the area.

DISCUSSION

Although we found that *R. raphanistrum* pollinators differed greatly in their effectiveness and efficiency, pollinator importance was determined primarily by visitation frequency rather than pollinator effectiveness, a common result found across plant species (Vazquez et al., 2005; Sahli and Conner, 2006). Despite the superior efficiency of large bees and Lepidoptera, the less efficient pollinators were the most important to plant reproduction simply because they were the most frequent visitors to *R. raphanistrum* during our study.

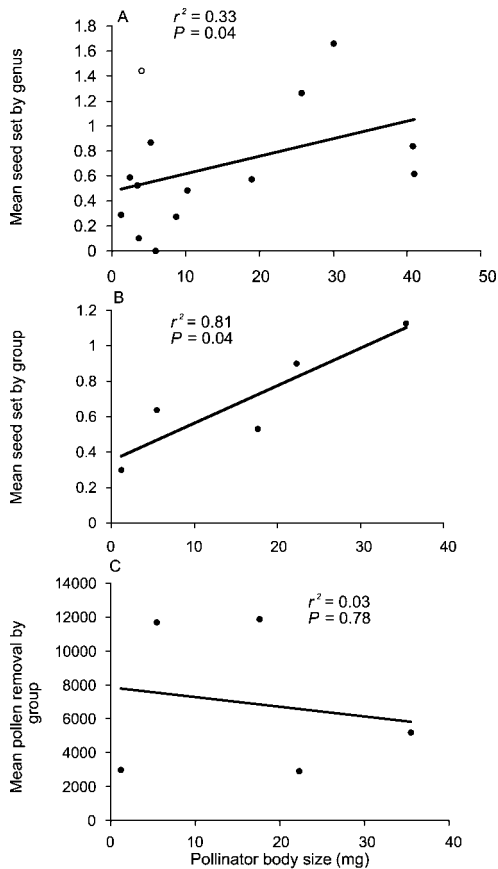


Fig. 4. Regressions of measures of effectiveness on body size. (A) Mean seed set effectiveness for each pollinating genus, (B) mean seed set effectiveness for the five pollinator groups (see Fig. 3), and (C) mean pollen removal effectiveness. Seed set and pollen removal effectiveness are the number of seeds set and pollen grains removed (respectively) during a single visit. Fitted line and r^2 values presented in (A) do not include the outlier *Ceratina* (open circle).

This result highlights the importance of characterizing the visitation rates of many visitors to plant species in order to determine which visitors are likely to be important for reproductive success. Measuring pollinator effectiveness and efficiency may not be as important and may actually obscure our understanding of pollinator importance if examined without visitation rates. However, in some populations and some species, effectiveness may prove important, especially when there is little variation among pollinators in visitation rates (Vazquez et al., 2005) or there are many completely ineffective pollinators (Schemske and Horvitz, 1989). Furthermore, measurements of effectiveness, when coupled with studies measuring natural selection by different pollinators and visitation rates, may tell us about past and current pollinator-mediated selection. For instance, there may be current selection on floral traits to make relatively ineffective pollinator species more effective at depositing pollen on stigmas, and past selection may have resulted in other pollinators being currently more effective at deposition.

Visitation determined most of the variation in pollinator importance because visitation to wild radish was extremely uneven. The small proportion (26%) of pollinators responsible for 81% of the reproduction in *R. raphanistrum* indicates that

TABLE 2. Percentage of visits to *Raphanus raphanistrum* by nine pollinator groups in 2001 and 2002. Small bees include *Augochlor-ella*, *Dialictus*, *Ceratina*, *Colletes*, and *Halictus*; large syrphid flies include *Syrpita*, *Syrphus*, and *Sphaerophoria*.

Pollinator	Visits (%)	
	2001	2002
Small bees	40.7	52.5
<i>Apis</i>	1.7	1.9
<i>Bombus</i>	1.3	0.6
<i>Thymelicus</i>	0.4	1.0
<i>Pieris</i>	7.7	0.9
<i>Toxomerus</i>	28.1	21.1
Large syrphid flies	11.9	14.1
<i>Allograpta</i>	3.2	0.8
<i>Eristalis</i>	4.9	7.3

this plant is not extremely generalized, relying on only four genera for most of its reproduction. In studies on some other plant species visited by a large number of taxa, a small percentage of the visitors were also found to be responsible for roughly 80–90% of total plant reproduction (e.g., Lindsey, 1984; Devall and Thien, 1989; Herrera, 1989; Gomez and Zamora, 1999). In other studies, some plants have more even pollinator assemblages (e.g., Pettersson, 1991; Kandori, 2002; Ivey et al., 2003), highlighting the importance of quantifying visitation evenness (Sahli and Conner, 2006).

Although only a minority of the visiting taxa were responsible for most of the plant reproduction during the 2 years of our study, it is unknown whether low visitation rates of other taxa were due to low densities of those taxa in the population we studied, competition with other plants for pollinators, or competition among pollinator taxa. Thus, a reduction in *Dialictus* or *Toxomerus* visits or a reduction in co-occurring flowering plants may increase visitation by previously less frequent taxa. For example, Ricketts (2004) found that seed set in coffee populations visited by many pollinator taxa was buffered against a decrease in the dominant honeybee because previously infrequent visitors increased in visitation rates with the loss of the dominant taxon. Therefore, the high number of taxa that are effective pollinators of *R. raphanistrum* may buffer this plant against shifts in pollinator assemblages across time and space, perhaps contributing to its success as a global weedy colonizer.

Results from this study also showed that differences in pollinator effectiveness can partially be explained by size, with larger pollinators effecting greater seed set. Kandori (2002) found the same relationship in *Geranium*. One exception to this trend in our study was *Ceratina*, a small, nonsocial bee that was an extremely effective pollinator. This pollinator was one of the few small pollinators that foraged for nectar, plunging its entire body into the tube of the flower to reach the nectar and possibly contacting the stigma more often. In fact, this species was never observed collecting pollen (H. Sahli, personal observation). The nectar-feeding behavior of this small bee is one possible explanation for its rather high effectiveness over that of similarly sized pollinators, which foraged primarily on pollen and thus perhaps mainly contacted the anthers.

Although body size can predict a pollinator's effectiveness at setting seeds, it is not predictive of a pollinator's ability to remove pollen. Because most of the pollinators of *R. raphanistrum* are primarily foraging on pollen, behavioral differences among pollinators in how they actively collect

pollen, which are unrelated to pollinator size, may have the biggest impact on pollen removal. The differences between pollinators in their pollen removal effectiveness and in their efficiency at transferring pollen were largely due to differences in feeding behaviors. Large bees and Lepidoptera removed the least pollen during a single visit, probably because they both feed primarily on the nectar of *R. raphanistrum*. Their low levels of pollen removal, coupled with their high seed set effectiveness (also correlated with larger size), resulted in a high pollinator efficiency, indicating that they do not need to remove much pollen in order to transfer pollen to a receptive stigma. Conversely, small bees and syrphid flies primarily feed on or collect pollen while visiting *R. raphanistrum*, which obviously results in the inefficient transfer of pollen grains from anthers to stigmas. Thus, our study indicates that pollinator effectiveness and efficiency are functions of both behavior and morphology.

All differences in pollen removal among pollinators occurred on anthers from long stamens, with pollinators not differing in their pollen removal effectiveness from anthers on short stamens. Previous studies have found that pollen removal from long-stamen anthers is greater than that from short-stamen anthers in plants with multiple stamen positions (Conner et al., 1995; Conner et al., 2003) and that pollen removal increases with increasing anther exertion (Murcia, 1990; Conner et al., 1995). Thus, all pollinators removed the same small proportion of pollen grains from short-stamen anthers. Stamen dimorphism in wild radish has been proposed as a mechanism to prevent pollen removal from inefficient pollinators, with the short stamens restricting the total number of pollen grains removed during a single visit (Conner et al., 2003). Findings from our study support this hypothesis because differences in pollen removal effectiveness among pollinators are eliminated on short stamens, thus reducing overall differences in pollinator efficiency. Further research on the maintenance of stamen dimorphism in the Brassicaceae is certainly needed.

There was surprisingly little temporal variation in the pollinator composition of *R. raphanistrum* during the 2 years of our study. Temporal variation in pollinator assemblages is often thought to be quite pronounced and can be responsible for changing selection pressure from year to year if taxa differ in their selection on traits. Indeed, other studies measuring temporal visitation, even on *R. raphanistrum*, have documented annual changes in pollinator assemblages with the most frequent visitor varying annually (Herrera, 1988; Schemske and Horvitz, 1988; Pettersson, 1991; Rush et al., 1995; Fishbein and Venable, 1996; Mahy et al., 1998; Kandori, 2002). Many of these past studies were also carried out over only 2 yr, yet they still found striking differences in the composition of the pollinator assemblage. Therefore, our findings are atypical in showing that pollinator assemblages were quite constant across 2 yr at our field sites. Based on our findings of little temporal variation in pollinators and previous estimates of pollinator-mediated selection on wild radish (Conner et al., 1996a, 1996b, 2003; Morgan and Conner, 2001), selection may be maintained across years, enabling a consistent response to selection and adaptation to pollinators.

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