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Source: *Ecology*, Vol. 77, No. 8 (Dec., 1996), pp. 2445-2457

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/2265745>

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A PLANT PATHOGEN INFLUENCES POLLINATOR BEHAVIOR AND MAY INFLUENCE REPRODUCTION OF NONHOSTS¹

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Abstract. Some plant pathogens attract pollinating insects and thus have the potential to influence the pollination of flowers, just as different flower species can influence one another's pollination. Showy, flower-like pseudoflowers caused by the rust fungus *Puccinia monoica* on *Arabis holboellii* (Brassicaceae) commonly co-occur with flowers of *Anemone patens* (Ranunculaceae). I evaluated the effects of pseudoflowers and anemone on each other's visitation, and the effect of pseudoflowers on the seed set of anemone. I expected that at low overall "flower" densities visitation would be facilitated in patches containing a mixture of these species. At low densities, pseudoflowers or flowers alone may be too rare to attract sufficient visitors, but the addition of the other species could make mixtures more attractive and thus increase visitation rates. At high densities I expected that "flowers" in mixtures would compete for pollinators because it is more energy efficient for pollinators to concentrate visits on the most rewarding species. I used artificial arrays to separate the effects of "flower" density and relative frequency on visitation. Local density was not a good predictor of the influence of one species on the other. Instead, visitation patterns depended most strongly on the kind of visitor (flies vs. bees). Visitation to *A. patens* by flies was facilitated by the presence of pseudoflowers at both high and low densities, whereas visitation to pseudoflowers was not significantly influenced by *A. patens* at either density. Local density affected visitation by bees, but relative frequency did not. In addition to observing visitation, I also quantified the effects of interspecific movement of both pollen and spores on the reproductive success of *A. patens*. Although the presence of pseudoflowers sometimes facilitates visitation to *A. patens*, this effect could be counterbalanced by competition through interspecific insect movement: sticky pseudoflowers remove pollen from visiting insects, and fungal spermatia deposited on flower stigmas reduce seed set.

Key words: *Anemone patens*; *Arabis holboellii*; competition; facilitation; floral mimicry; fly pollination; halictid bees; *Puccinia monoica*; *Pulsatilla patens*; rust fungi.

INTRODUCTION

Plant pathogens that attract pollinating insects may affect the reproductive success of other species in the community besides their hosts, just as different flower species can influence one another's pollination. We do not know how often plant pathogens attract pollinators, but evidence is beginning to accumulate that it may be relatively common (Craigie 1927, 1931, Buller 1950, Savile 1976, Batra and Batra 1985, Batra 1987, 1991, Vánky 1987, Bultman and White 1988, Wilding et al. 1989, Patt 1992a, Bultman et al. 1993, 1995, Roy 1993, 1994a, b). For example, three species of crucifer rusts (*Puccinia monoica*, *P. thlaspeos*, and *P. consimilis*) form flower-mimicking pseudoflowers on their hosts, which attract insects that help the fungus reproduce (B. A. Roy 1993, 1994b, unpublished data). The crucifer rusts infect at least eight common genera in the Brassicaceae (Farr et al. 1989, Roy 1993, 1994b), for a total of ≈960 host species worldwide. Crucifer rusts are not the only rust fungi that are likely to attract pollinators,

since most rust fungi produce spermatia (fungal gametes; equivalent to sperm or pollen) in a sweet-smelling, sugary liquid (Buller 1950, Savile 1976). If even a small fraction of the ≈60 000 other species of rust fungi attract pollinators, the effect on flower pollination could be significant. In addition to the pathogens that use insects as "pollinators" to transfer gametes, there are also several pathogens that use pollinators as vectors to transfer infectious spores. This group includes the flower-infecting anther smuts, which inhabit flowers in at least five different plant families (Vánky 1987), and the mummy-berry fungi, which infect many species in the Ericaceae (Batra and Batra 1985, Batra 1987, 1991).

In this study I asked whether fungal pseudoflowers caused by *Puccinia monoica* infecting *Arabis holboellii* influenced visitation and seed set of the flower *Anemone patens* (hereafter referred to as anemone), and whether anemone influenced visitation to pseudoflowers. I chose to examine the pseudoflower-anemone association for several reasons. First, pseudoflowers are exceptionally attractive to insects because they look and smell like flowers and they produce copious nectar (Roy 1993). Second, anemone and pseudoflowers are commonly associated throughout western North Amer-

¹ Manuscript received 1 June 1995; revised 15 January 1996; accepted 30 January 1996; final version received 4 March 1996.

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ica (B. A. Roy, *personal observation*), into Alaska (W. S. Armbruster, *personal communication*), and probably also in Europe wherever *Arabis* and anemone have overlapping ranges. Third, these early spring species are often the only species "flowering" at a site, and thus their interactions with pollinators should be relatively easy to quantify. Fourth, I knew from previous work that anemones and pseudoflowers are visited by the same flies and bees (Roy 1993). And fifth, although flower-like, pseudoflowers do not resemble anemone flowers in either appearance or scent, so insects should be able to discriminate between them.

The first question I asked was: do pseudoflowers and anemone influence each other's visitation? Whether flowers of different species have a negative or a positive effect on each other's visitation depends on the foraging decisions that insects make based on the resources that are present. For example, both flower density and flower frequency can influence insects' ability to recognize and locate flowers, and their choice of flower can be influenced by the quality of the reward and the ease of extracting it (Heinrich and Raven 1972, Pyke 1980, Pleasants 1981, Rathcke 1983, Stephens and Krebs 1986, Feinsinger 1987, Sih and Baltus 1987, Kunin 1993, Dreisig 1995). To separate the effects of "flower" density and "flower" frequency (hereafter referred to as plot composition) on visitation I used a factorial design and artificial arrays of flowers and pseudoflowers. To determine whether the patterns of insect behavior regarding density and frequency were consistent among sites and throughout the season, I performed the same experiment at three different sites and at three different times during the season.

I expected that my visitation results would fit a model proposed by Rathcke (1983) for flower mixtures. She suggested that at low densities facilitation of pollination should occur in mixtures, whereas at high densities competition should occur. At low densities, flowers of a particular species may be too rare to attract many visitors, but when found in combination with another species more visitors should be attracted (Straw 1972, Bobisud and Neuhaus 1975, Rathcke 1983, Thomson 1983, Feinsinger 1987). On the other hand, when densities are high, it is more energy efficient for pollinators to concentrate their visits on the most rewarding species, and competition for visitation should occur (Rathcke 1983, Feinsinger 1987).

The second major question I asked was: does interspecific movement by pollinators interfere with pollination? Even though visitation rates may increase with increasing overall floral densities, if insects move between species, pollination quality may decrease because pollen is being deposited on the wrong species. This kind of competition has been referred to as improper pollen transfer (Rathcke 1983, Kunin 1993) or interspecific pollen transfer (Waser 1978a, b, Galen and Gregory 1989). I will refer to it simply as interspecific transfer because it is possible that movement of spores

between flowers and fungi may also reduce effective pollination. For example, fungal spores deposited on stigmas might interfere with fertilization leading to a decrease in effective pollination, or pollen could be transferred to the fungus where it is wasted.

To assess whether interspecific movement by insects interfered with pollination, I broke the question into several subquestions and experiments. First I quantified interspecific pollinator movement during the visitation experiments outlined above. Two measures were used: (1) pollinator preference, which is a measure of how often one species is visited relative to another; preference gives an indication of how well a species competes for visitation, and (2) pollinator constancy, which is an index of how often a particular visitor flies between "flower" species (Waser 1986). I next performed separate experiments to quantify the potential for pollen loss from anemones to pseudoflowers. Finally, I measured seed set in the presence and absence of pseudoflowers. Seed set is an ultimate measure of whether differences in visitation mattered. For example, it is possible that differences in insect behavior regarding flower species may not translate into differences in seed set, if each flower nonetheless had sufficient visitation to achieve full seed set.

NATURAL HISTORY AND LOCALITIES

Puccinia monoica Arth. is a rust fungus that infects species in seven different genera of the Brassicaceae (Farr et al. 1989). The infected species studied here, *Arabis holboellii* var. *retrofracta* (Grah.) Rydberg, is a widespread herbaceous perennial in Arctic and montane regions of the northern hemisphere (Rollins 1941). Infection of *A. holboellii* by *P. monoica* occurs in late summer from wind-borne basidiospores produced on the primary host (Roy and Bierzychudek 1993), the grass *Koeleria macrantha* (Ledeb.) Schultes (synonyms = *K. nitida* and *K. cristata* [Arnou 1994]). Within a few months of basidiospore germination and penetration of *Arabis* leaves, the hyphae invade the meristematic tissue and cause systemic infection. Infected *Arabis* plants produce one to several flower-like rosettes (pseudoflowers) in the spring, but rarely produce true flowers (Roy 1993). The reproductive structures of the rust fungus, spermatogonia containing spermatia and receptive hyphae, form on the surface of the pseudoflowers. Insects are required to transfer spermatia to receptive hyphae belonging to a different mating type (Roy 1993). Insect exclusion experiments show that visitation is necessary for rust reproduction, and that multiple visits may increase the likelihood of sexual spore formation (B. A. Roy 1993, *unpublished data*).

Anemone patens (L.) Miller (synonym = *Pulsatilla patens* [Hoot et al. 1994]), commonly known as pasque flower or anemone, is a member of the Ranunculaceae. It is common in boreal and alpine areas throughout the northern hemisphere (Harrington 1954). In the early

spring plants bear one to many large (40–80 mm diameter), showy blue flowers that resemble crocus flowers. A pilot study (B. A. Roy, unpublished data) showed that visitation by insects is important for the reproduction of *A. patens*. Flowers can set seed without visitation, but seed set increased over threefold when insects are allowed to visit. Outcross pollen was more effective than self pollen alone, further indicating a role for insect visitation.

Three sites at similar elevations (≈2700 m) were located in Gunnison County, Colorado. The Cement Creek and Roadside sites are, respectively, 4.0 and 5.0 km along the Cement Creek road from its intersection with U.S. highway 135. The One Mile site is at the One Mile campground 11.5 km east of Almont on the Taylor River road, ≈8 km from Cement Creek. *Artemisia tridentata* was the dominant plant at all three study sites.

DO PSEUDOFLOWERS AND ANEMONE INFLUENCE EACH OTHER'S VISITATION?

Methods

I measured insect visitation at all three sites in 1993. Because date of first flower varied due to different snow cover and melt dates, I standardized observation times by flowering stage. During "early phenology" observations 30–40% of anemones were flowering, and pseudoflowers were fresh and strongly scented. During "middle phenology" ≈50% of anemones were flowering, and during "late phenology" >90% of anemone were flowering and pseudoflowers were drying out and losing their scent.

I prepared the sites for observation by first removing all flowers and pseudoflowers from six 1-m² treatment plots, spaced 5 m apart along a linear transect. In these plots I arranged freshly picked anemone flowers and pseudoflowers in rectangular arrays of florists' pics (small plastic vases). The heights of flowers and pseudoflowers were similar to each other and to naturally occurring flowers. Wilted flowers were replaced as necessary. The treatments included two combinations of density (high and low), and two combinations of frequency (1:0 and 50:50) for each of the two species for a total of six treatments (Fig. 1). The high-density treatments contained 12 "flowers"/m² plot, and low-density treatments contained 6 "flowers"/m². These densities were similar to naturally occurring patches, which ranged from 6.5 to 10.5 "flowers"/m².

A replicate consisted of 20 min of observation at each of the six plot types. Because there were six treatments, but only three observers, observers were randomly assigned to treatment plots for one 20-min observation period, then randomly assigned among the remaining three treatments for another observation period. Each pair of observation periods therefore constitutes a replicate during which visitation to each of the treatments was tallied for 20 min. To remove bias

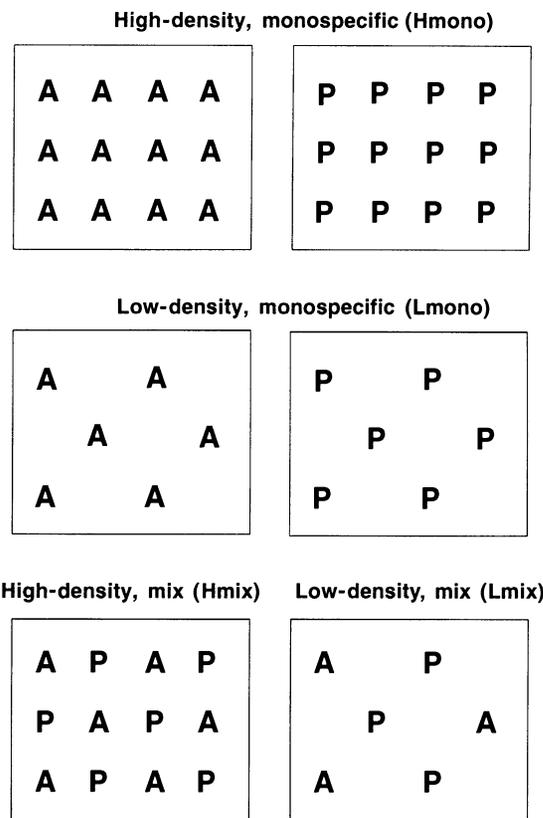


FIG. 1. Composition of the artificial arrays. A = *Anemone patens* flowers, P = fungal pseudoflowers on *Arabis*.

due to plot position, the order of the treatment plots along the transect was rearranged after each complete set of six (i.e., after each replicate) had been observed. Between two and five (mean of four) replicates were observed per site per phenological stage. Observations were made between 1000 and 1500 local time, under clear to partly cloudy skies.

Visitation rates were determined in two ways. To examine the role of overall plot density on insect attraction, I calculated visitation to all "flowers" within a plot for an overall arrival rate (number of arrivals to a plot per hour). To examine the probability of individual flowers being visited, I calculated per "flower" visit rates (number of insect visits per "flower" per hour). For example, if over the course of an hour six insects each visited one "flower" in a plot containing 12 flowers, the arrival rate would be 6 arrivals/h, and the per "flower" visit rate would be 6 visits·12 flowers⁻¹·h⁻¹ = 0.5 visits·"flower"⁻¹·h⁻¹.

Pollinator preference for flowers vs. pseudoflowers was determined by counting the total number of visits to each species, and then calculating the logarithm of the following preference index (Cock 1978):

$$\frac{\text{no. visited of sp. 1} / \text{total no. of sp. 1}}{\text{no. visited of sp. 2} / \text{total no. of sp. 2}}$$

In addition to counting the number of visits per "flower" I also timed the duration of each visit to the nearest second. A visit was counted only if the insect was observed on anthers or stigmas; standing on petals or uninfected leaves was neither counted nor timed. Average visit duration per "flower" was calculated as the number of seconds per number of "flowers" in the plot. Different visitor species are likely to spend different amounts of time on "flowers." Therefore, I also estimated the average duration of a single visit ($[\text{number of seconds}]/[\text{number of visits}]$) for all visitor types. For example, suppose that during an observation period two insects entered a plot containing 10 flowers. One insect then spent 3 s on a flower and the other 6 s. Average visit duration per flower is then $3+6\text{ s}/10\text{ flowers} = 0.9\text{ s/flower}$, and the average duration per visit is $3+6\text{ s}/2\text{ visits} = 4.5\text{ s/visit}$. To explore variation in duration per visit for common visitors (>10 visits to each species), I used a two-way Kruskal–Wallis ANOVA with "flower" visited and visitor type as main effects, and duration per visit as the dependent variable (the Kruskal–Wallis test was used because the variances were heteroscedastic). Since there was a strong "flower" by visitor interaction, I also performed pairwise tests for each common visitor–flower combination, applying the Bonferroni criterion to set the critical alpha level (Sokal and Rohlf 1981).

The visitors to these species are primarily flies and bees. Because the behavior of these two groups might differ, and the ratio of flies:bees varies from year to year, I performed separate analyses for flies and bees. Visit number and visit duration per "flower" were strongly positively correlated (Pearson's $r = 0.7$ or greater) so I analyzed these response variables together in a MANOVA. I refer to the combination of visit number and visit duration per "flower" as a single variable called "visitation" because MANOVA used information from both variables to construct a single statistic. When decomposing effects on visitation, I separately refer to number of visits per "flower" and duration of visits per "flower" only when it clarifies the analysis. Both visit variables were square-root transformed before analysis to achieve normally distributed residuals.

The data set was unbalanced because I was unable to make observations during the middle of the flowering season at Cement Creek. Rather than discard data to achieve balance, I chose to do two separate MANOVAs for each visitor type. One MANOVA uses data from all three sites, but includes only the early and late phenologies, whereas the other MANOVA uses data from the two sites (Roadside and One Mile) for which there were three observation periods. When it was necessary to perform separate contrasts, such as in the analyses where there were three possible sites, or to dissect a significant interaction, I used the Bonferroni criterion to set the critical alpha level (Sokal and Rohlf 1981). I used the statistical program JMP, Version 3.0 (SAS 1994) for all analyses.

Results

The visitor fauna was composed of ≈ 28 species, most of which visited both *Anemone patens* and pseudoflowers (Table 1). However, different insect taxa tended to visit one kind of "flower" more than the other. For example, sepsid, muscid, and anthomyiid flies preferred pseudoflowers, whereas syrphid flies and an agromyzid fly (which was grouped with "small flies" in Table 1) tended to visit anemone more often (Table 1). Halictid bees, on the other hand, visited anemone much more often than pseudoflowers: 92.8% of their 2036 visits were to anemone. There were only minor differences in the kinds of visitors present at the three sites (Table 1).

Although pseudoflowers and anemone were visited by the same kinds of visitors, pseudoflowers received only 29.4% of 4182 recorded visits, and received fewer visits than anemone on every day of observations (Table 1), yielding an overall preference for anemone of +0.37. However, bees and flies had very different preferences. Bees, especially halictid bees, showed a strong preference for anemone (Table 1, Fig. 2) with a preference index of +0.83. Flies, on the other hand, visited pseudoflowers a little more often than anemone (925 visits to 919), yielding a very slight negative preference index for anemone of -0.003 .

Visit duration per "flower" can be large either because a particular visitor type made many visits and the cumulative sum is therefore large, or because the average length of a visit is long. Because bees made so many visits to anemone flowers during an observation period, the duration per "flower" was typically high (Fig. 3). However, the average duration of a single visit to flowers was much shorter than that to a pseudoflower (Table 2). An ANOVA with "flower" species and visitor type as the main effects and visit duration of a single visit as the dependent variable, showed that there were significant differences in overall visit duration per visit to the two "flowers" ($F_{1,4091} = 36.00$, $P < 0.0001$), in duration per visit by the different visitors ($F_{7,4091} = 29.98$, $P < 0.0001$) and a significant interaction between "flower" and visitor type ($F_{7,4091} = 31.46$, $P < 0.0001$). Anthomyiid flies, muscid flies, sepsid flies, "small flies," and some bees spent significantly more time on pseudoflowers, but only halictid bees spent more time on anemone. Ants and syrphids spent the same amount of time per visit on both pseudoflowers and flowers (Table 2).

Plot composition significantly influenced visitation by flies. Per "flower" visitation by flies was significantly greater in mixtures (main effect of plot composition; Table 3, Figs. 2a and 3a). Fly response to plot composition differed for anemone and pseudoflowers (significant species by plot composition interaction; Table 3). Pseudoflowers facilitate fly visitation to anemone, both through fly visit number per anemone flower (Fig. 2a) and especially through visit duration per flow-

TABLE 1. Visitors to pseudoflowers (pseudo.) and *Anemone patens* at three sites and at three different times of the season as defined by *Anemone* phenology (E = Early, M = Middle, L = Late). Visitors are listed by family names when it was possible to identify them; otherwise, the columns are headed with Unid. (for unidentified).†

Phenology/ Species	Anth. fly	Musc. fly	Sarc. fly	Scat. fly	Seps. fly	Syrp. fly	Tach. fly	Teph. fly	Small fly	Unid. fly	Hal. bee	Other bee	Form. ant	Unid. wasp	But- ter fly	Elat. bee- tle	Unid. unk.	Total
Cement Creek																		
E/ <i>Anemone</i>	7	1	0	0	25	3	1	0	38	3	453	11	7	1	1	0	0	551
E/pseudo.	12	4	0	0	67	2	0	0	3	0	47	9	63	0	0	0	0	207
L/ <i>Anemone</i>	21	0	0	0	16	25	2	0	178	0	280	2	13	0	2	0	4	553
L/pseudo.	36	6	0	0	66	6	0	0	2	0	13	1	18	0	0	0	0	148
One Mile																		
E/ <i>Anemone</i>	0	0	0	0	86	57	0	0	5	1	148	4	8	0	0	0	3	312
E/pseudo.	1	4	0	0	151	4	0	0	1	0	17	0	0	0	0	0	0	178
M/ <i>Anemone</i>	2	7	0	0	5	0	0	0	1	0	24	0	7	0	0	0	0	46
M/pseudo.	0	3	7	0	11	0	3	0	5	0	2	0	0	0	0	0	0	31
L/ <i>Anemone</i>	0	1	0	0	0	57	2	0	2	0	284	23	8	0	4	0	0	383
L/pseudo.	1	1	0	0	3	2	1	0	6	1	32	6	14	0	0	1	0	68
Roadside																		
E/ <i>Anemone</i>	39	26	1	1	21	11	0	0	1	0	1	2	0	0	0	0	0	103
E/pseudo.	22	23	1	16	29	8	2	0	2	3	0	0	0	0	0	0	0	106
M/ <i>Anemone</i>	11	15	0	0	90	19	0	1	21	0	281	4	6	4	0	0	0	452
M/pseudo.	8	4	3	0	271	7	0	3	5	0	11	2	11	0	1	0	0	326
L/ <i>Anemone</i>	6	1	0	0	72	19	0	0	18	0	419	20	9	0	0	0	0	564
L/pseudo.	8	4	0	0	92	2	0	0	2	1	24	11	21	0	0	0	1	166
Total	174	100	12	17	1005	222	11	4	290	9	2036	95	185	5	8	1	8	4182

† Anth. = Anthomyiidae (2–3 spp.), Musc. = Muscidae (one sp.—a Calliphorid look-alike), Sarc. = Sarcophagidae (one sp.), Scat. = Scatophagidae (two spp.), Seps. = Sepsidae (one sp.), Syrph. = Syrphidae (two spp.), Tach. = Tachinidae (2–3 spp.), Teph. = Tephritidae (one sp.), “Small fly” (several small flies including: a common species in the Agromyzidae, one sp. Chloropidae, one sp. Sciaridae), Unid. = Unidentified, Hal. = Halictidae (two spp.), Other bee (three spp., primarily Andrenidae), Butterfly (three spp.), Elat. = Elateridae (one sp.).

er (Fig. 3a). In contrast, anemone flowers had little effect on fly visitation to pseudoflowers (Figs. 2a and 3a). Plot composition did not significantly influence visitation by bees to either anemone or to pseudoflowers (no plot composition effects; Table 4, Figs. 2b and 3b), although there was a trend toward more visits and visits of longer duration in low-density treatments.

Overall, visitation to plots was positively density dependent with high-density plots having higher insect arrival rates (Fig. 4a). However, low-density plots consistently received more visits per “flower” (Fig. 4b). Visit duration per flower was higher in low-density plots than in high-density plots (Fig. 3a, b; Table 4).

Although visitation to the treatments remained relatively consistent among sites, other patterns emerge in the data over the course of the flowering season (significant effect of phenology in Tables 3 and 4). The number and duration of visits per “flower” by flies were the highest during the middle of the flowering season and the lowest during the late phenological observations (Figs. 2e and 3e). Visits per “flower” by bees increased over the season (Fig. 2f) and because duration per “flower” was highest during the middle observation period (Fig. 3f). The increase in visit duration per “flower” but not in visit number during the middle part of the season probably reflects the reluctance of insects to fly when it is cold—the middle ob-

servations were made the day after a storm moved through.

For bees there was a significant phenology by species interaction (Table 4); bee visitation to pseudoflowers was fairly even across the season, whereas anemone had greater visitation late in the season. Bee visitation also varied among the sites depending on phenology; visit number by bees increased over the season at Roadside and One Mile, but decreased at Cement Creek (Table 1).

DOES INTERSPECIFIC MOVEMENT OCCUR?

Methods

An important measure of interspecific movement is constancy, which is the tendency of individual pollinators to specialize on a particular flower species when foraging even though this specialization varies among individuals (Waser 1986). Individuals that primarily move between flowers of a particular species, even though equally rewarding species are skipped in the process, are said to be constant, whereas individuals that often switch between flower species are said to be inconstant. A high degree of constancy can result in competition for visitation in mixtures, whereas inconstant foraging can lead an increase in interspecific transfer (Waser 1978a, b, 1986, Rathcke 1983, Campbell 1985, Campbell and Motten 1985, Kunin 1993). I

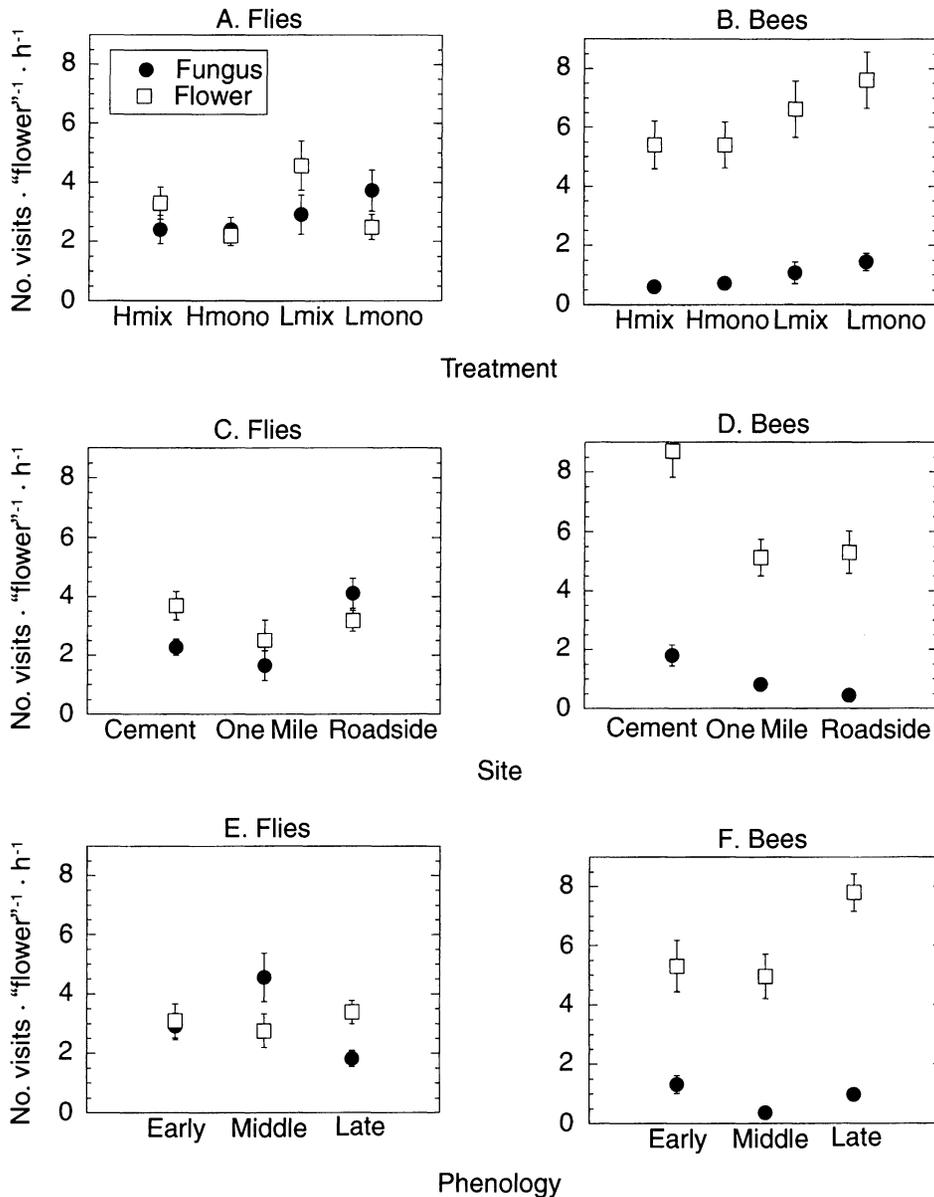


FIG. 2. Mean number of visits per "flower" per hour shown separately for pseudoflowers and *Anemone patens*. (A) Number of fly visits per "flower" per hour for each treatment. The treatments are: Hmono = high-density monospecific plots, Hmix = high-density mixtures, Lmono = low-density monospecific plots, Lmix = low-density mixtures. (B) Number of bee visits per "flower" per hour for each treatment. (C) Number of fly visits per "flower" per hour for each site. (D) Number of bee visits per "flower" per hour for each site. (E) Number of fly visits per "flower" per hour for each observation period during the season (phenology). (F) Number of bee visits per "flower" per hour for each phenological observation period.

estimated constancy by following individual insects in the mixed arrays (Fig. 1) and counting transitions between pseudoflowers and anemone. From the transition data, I calculated Bateman's constancy index (Bateman 1951, Waser 1986) summed over all visitors, and individually for those insect taxa for which transitions were observed for >10 individuals.

Results

Insect groups differed in constancy as measured with Bateman's index "C." Eighty-six percent of all tran-

sitions (339/393) were made by halictid bees and syrphid flies; of these two groups, halictid bees were moderately inconstant ($C = -0.25$, transitions = 144, individuals = 90), whereas syrphid flies were moderately constant ($C = 0.21$, transitions = 195, individuals = 51). For the other visitor types, there were too few transitions by too few individuals (<10) to calculate constancy individually, but summing all transitions gives an overall constancy index of $C = 0.22$ (transitions = 393, individuals = 167).

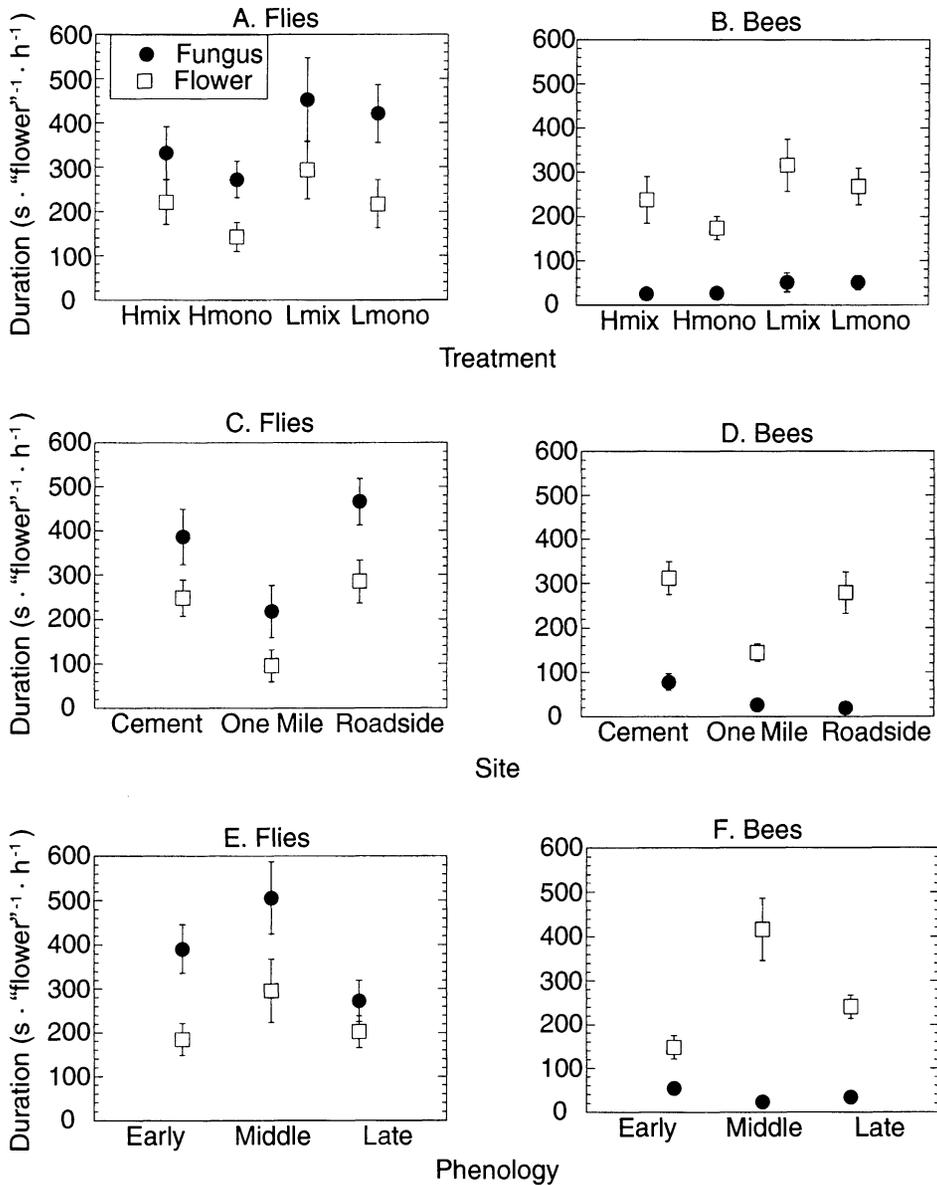


FIG. 3. Mean visit duration (s) per "flower" per hour shown separately for pseudoflowers and *Anemone patens*. (A) Fly duration (s) per flower per hour for each treatment. Treatment abbreviations are the same as Fig. 2. (B) Bee duration (s) per "flower" per hour for each treatment. (C) Fly duration (s) per "flower" per hour for each site. (D) Bee duration (s) per "flower" per hour for each site. (E) Fly duration (s) per "flower" per hour for each observation period during the season (phenology). (F) Bee duration (s) per "flower" per hour for each phenological observation period.

DOES INSECT MOVEMENT BETWEEN FLOWERS AND PSEUDOFLOWERS RESULT IN POLLEN LOSS?

Methods

Interspecific movements of insects lead to the potential for pollen to be transferred to the wrong species where it will be completely ineffective. In 1993 I performed an experiment to determine whether the sticky surfaces of infected leaves could remove pollen from visitors, and thus remove it from the pollen pool. Before the rust fungus became sexually receptive at Ce-

ment Creek, I excluded 14 pseudoflowers from insect visitation by caging them (as in Roy 1993). After the fungus became receptive, I removed cages, one at a time, from 12 of the pseudoflowers and allowed one insect to visit each one; the other two pseudoflowers were controls to which no visitors were allowed. I estimated the number of pollen grains deposited by placing the entire infected pseudoflower in a vial with 10 mL of distilled water and shaking it violently, then drawing out two 1-mL samples with a pipette. Pollen present in each sample was counted in a Sedgewick-

TABLE 2. Mean visit duration for the eight groups of insects that made ≥ 10 visits to both pseudoflowers (fungus) and *Anemone patens* (flower).

Visitor		Time (s) on pseudoflower		Time (s) on anemone		K-W test†
Order	Family	$\bar{X} \pm 1$ SE	<i>n</i>	$\bar{X} \pm 1$ SE	<i>n</i>	
Diptera	Anthomyiidae	258 \pm 30.0	88	73 \pm 14.4	86	$P \leq 0.006$
	Muscidae	126 \pm 24.8	49	63 \pm 14.4	51	$P \leq 0.006$
	Sepsidae	96 \pm 5.4	690	69 \pm 6.8	315	$P \leq 0.006$
	Syrphidae sp. A	43 \pm 19.4	28	29 \pm 3.6	182	NS
	Unid. small flies	337 \pm 78.3	26	97.3 \pm 11.0	264	$P \leq 0.006$
Hymenoptera	Halictidae	24 \pm 4.1	146	37 \pm 1.5	1889	$P \leq 0.006$
	Formicidae	48 \pm 5.0	127	50 \pm 12.3	58	NS
	Other bees‡	63 \pm 18.7	29	25 \pm 4.2	64	$P \leq 0.006$

† Kruskal–Wallis test. Significance levels were Bonferroni corrected for eight tests (= significant at 0.006 or less).

‡ Primarily Andrenidae.

rafter counting chamber. The two samples were averaged and the mean was multiplied by 10 (for the 10-mL total) for an estimate of number of pollen grains removed by pseudoflowers.

To estimate how much pollen could be lost when insects landed on a pseudoflower after visiting a flower I needed to know what average pollen loads were. In 1994, I estimated average load for three common insect visitors (a sepsid fly, a muscid fly, and a halictid bee) by counting the grains of anemone pollen on 7–10 individuals under a dissecting microscope. To facilitate pollen identification, I caught the insects as they emerged from anemone flowers in a meadow along Cement Creek where there were no other flowers blooming. Because some of the muscid flies, which are extremely hairy, had more pollen on them than I could

count individually, I was forced to estimate numbers in the 3/10 cases where there were >1500 grains.

Results

Interspecific pollen transfer from anemone to pseudoflowers occurs: 77% of the visitors that were allowed a single visit to a pseudoflower deposited anemone pollen on it during the visit. Halictid bees ($n = 6$) left an average (± 1 SE) of 48 ± 16.9 pollen grains in a single visit, or about a fifth of their normal load (227 ± 98.5 grains; Table 5). Sepsid flies ($n = 7$) left 10 ± 4.2 grains per visit, or about one-third of their normal load (32 ± 13.8 grains; Table 5). Control (caged) pseudoflowers had no pollen on them. Since insects deposit pollen on pseudoflowers from the same places (legs, thorax, abdomen) that they deposit pollen on anemone

TABLE 3. MANOVA on fly visitation (a composite variable including number of visits by flies/flower and time/flower by flies). All main effects are shown, but only the significant interactions.

Source	Pillai's trace	<i>F</i>	df		<i>P</i>
			Num.	Den.	
A) MANOVA for all three sites during the early and late parts of the flowering season					
Species	0.24	25.26	2	159	<0.0001
Plot composition	0.05	4.62	2	159	0.0112
Plot density	0.05	3.78	2	159	0.0248
Site	0.13	5.46†	4	320	0.0003
Phenology	0.06	5.10	2	159	0.0071
Composition \times site	0.06	2.57†	4	320	0.0381
Composition \times species	0.09	7.91	2	159	0.0005
Site \times phenology	0.38	18.92†	4	320	<0.0001
Composition \times species \times site \times phenology	0.08	3.58	4	320	0.0071
B) MANOVA for the two sites (Roadside and One Mile) for which there were observations during the early, middle, and late parts of the flowering season (= phenology)					
Species	0.14	11.13	2	142	<0.0001
Plot composition	0.04	3.03	2	142	0.0517
Plot density	0.04	2.89	2	142	0.0589
Site	0.10	7.57	2	142	0.0008
Phenology	0.20	7.95†	4	286	<0.0001
Composition \times species	0.06	4.39	2	142	0.0141
Site \times phenology	0.32	13.85†	4	286	<0.0001
Composition \times species \times site \times phenology	0.07	2.48†	4	286	0.0445

† Approximate *F* test.

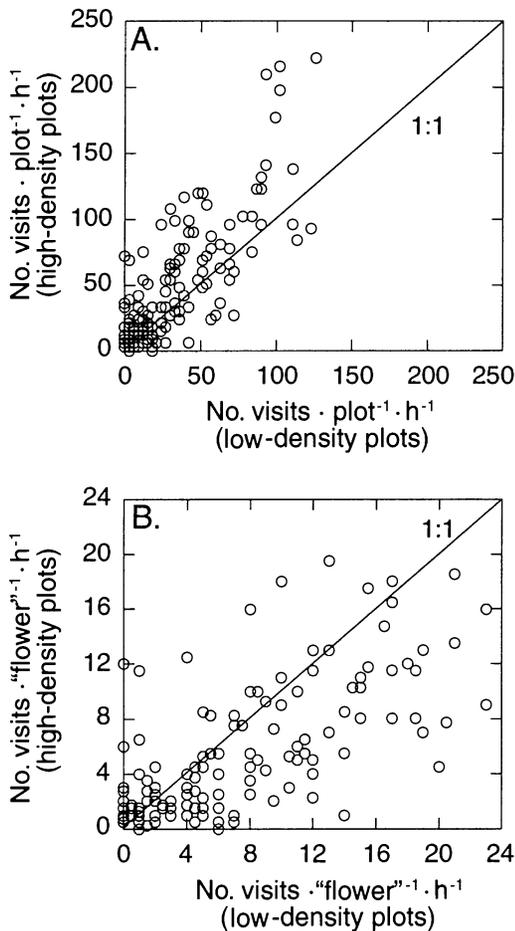


FIG. 4. Density-dependent visitation. (A) Visitor arrival rates in high-density plots vs. low-density plots. (B) Visitation rates per flower in high-density plots vs. low-density plots. A 1:1 relationship is indicated by a diagonal line.

flowers, loss to pseudoflowers is very likely to have a negative impact on anemone pollination.

DOES THE PRESENCE OF FUNGAL SPERMATIA ON FLOWER STIGMAS AFFECT SEED SET?

Methods

To determine whether the presence of fungal spermatia on stigmatic surfaces affected seed set of anemone, I performed a pollen and spermatia augmentation experiment in 1993. In this experiment, I compared seed set of the treated flowers to both open- and hand-pollinated controls on the same plants. I located 23 plants of anemone with 4–5 buds, and randomly assigned each of three buds to one of three treatments: (1) open-pollinated; (2) bagged, spermatia + pollen at the same time; (3) experimental control. The bud was covered as in (2), then the flower was outcrossed with the pollen of nearby flowers applied with a small paintbrush.

For statistical analysis, I used a mixed-model ANO-

VA with treatment as a fixed effect and plant as a random effect with the number of viable seeds square-root transformed as the dependent variable. The flowers on six plants froze during the experiment, so they were dropped from the analysis, leaving a sample of 17. I used a priori contrasts to separate the means. To determine whether there was a difference in seed set between hand-pollinated or insect-pollinated flowers, I contrasted the experimental controls with the open-pollinated flower. To determine whether there was a difference in seed set between flowers that only received hand-applied pollen and flowers that received both spermatia and pollen, these two treatments were contrasted.

Results

When spermatia and pollen were applied at the same time, there was a significant decrease in seed set relative to the hand-pollinated controls (Fig. 5; $F_{1,17} = 4.74$, $P = 0.03$). There was no significant difference between the hand-pollinated controls and insect-pollinated flowers ($F_{1,17} = 0.01$, $P = 0.92$), indicating that hand-pollination did not damage the flowers.

DOES THE PRESENCE OF PSEUDOFLOWERS ACTUALLY AFFECT ANEMONE REPRODUCTION IN THE WILD?

Methods

To determine whether the presence of pseudoflowers affected seed set in the wild, and not just in manipulated experiments, I compared the reproduction of anemone next to infected and uninfected *Arabis* plants in 1993. First, I located pseudoflowers with an adjacent (within 10 cm) anemone plant at Roadside (19 pairs) and Cement Creek (23 pairs). I then divided the pseudoflower–anemone pairs into two treatments. In the “infected” treatment, neither plant was manipulated. In the “uninfected” treatment, I removed the pseudoflowers from infected *Arabis*, leaving behind normal-looking leaves. Manipulating infected plants to make them appear uninfected (rather than choosing anemone individuals with uninfected *Arabis* neighbors) controls for possible confounding microsite differences (such as higher water availability) between naturally uninfected and infected plants that may in themselves influence seed set. Each anemone plant had 2–4 flowers. Seed set was measured for the flower nearest to the pseudoflower in the infected treatment, or the flower nearest to the “uninfected” plant in the uninfected treatment. To determine whether seed set was pollinator limited, I hand-pollinated one flower on each of the anemone plants in the “infected” and “uninfected” neighbor pairs. I tested for an effect of uninfected vs. infected neighbors on seed set in an ANOVA with neighbor as a fixed effect and site as a random effect. The dependent variable was the difference in number of seeds between the hand-pollinated and the naturally visited flower.

TABLE 4. MANOVA on bee visitation (a composite variable including number of visits by bees/flower and time/flower by bees). All of the main effects are shown, but only the significant interactions.

Source	Pillai's trace	F	df		P
			Num.	Den.	
A) MANOVA for all three sites during the early and late parts of the flowering season					
Species	0.46	92.89	2	159	<0.0001
Plot composition	0.98	1.34	2	159	NS (0.2636)
Plot density	0.04	3.74	2	159	0.0260
Site	0.33	15.55†	4	320	<0.0001
Phenology	0.07	6.21	2	159	0.0025
Site × phenology	0.42	21.83†	4	320	<0.0001
Phenology × site	0.07	6.37	2	159	0.0022
Phenology × species × density	0.04	3.08	2	159	0.0486
B) MANOVA for the two sites (Roadside and One Mile) for which there were observations during the early, middle and late parts of the flowering season (= phenology)					
Species	0.62	115.36	2	142	<0.0001
Plot composition	0.01	0.78	2	142	NS (0.4609)
Plot density	0.05	3.63	2	142	0.0291
Site	0.01	0.64	2	142	NS (0.5282)
Phenology	0.59	30.25†	4	286	<0.0001
Site × phenology	0.37	16.22†	4	286	<0.0001
Phenology × species	0.39	17.37†	4	286	<0.0001
Site × phenology × species	0.25	10.05†	4	286	<0.0001

† Approximate F test.

Results

The presence of pseudoflowers influenced the seed set of anemone, but did so differently at the two sites. In a two-way ANOVA with the difference between hand-pollinated and open-pollinated flowers as the dependent variable, the main effects of site and neighbor were not significant, but there was a significant site by neighbor interaction ($F_{1,21} = 13.14, P = 0.0019$). Anemone set significantly more seed when adjacent to infected plants at Cement Creek ($F_{1,21} = 11.02, P = 0.0038$). At the Roadside site, there was a tendency for the opposite pattern to be true; more seed was set when anemone were adjacent to uninfected plants ($F_{1,21} = 2.75, P = 0.1146$).

Competition through pollinator preference can only affect female fitness if seed set is limited by visitation. Pollinators were limiting only at Cement Creek where there was a significant positive effect of hand-pollination (an average increase of 10.7 seeds). At the Roadside site there was a slight, but not statistically significant, negative effect of hand pollinations (-3.3 seeds).

DISCUSSION

The effect of pseudoflowers on Anemone patens

I expected that facilitation of visitation per "flower" would occur at low densities, and that at high densities,

TABLE 5. Mean number of pollen grains per naturally foraging insect.

Insect	n	Mean ± 1 SE
Halictid bees (one sp.)	10	227 ± 98.5
Sepsid flies (one sp.)	7	32 ± 13.8
Muscid flies (one sp.)	9	1115.78 ± 332.87

competition for visitation would occur. Neither of these predictions were supported by the data. Mixtures facilitated fly visitation at both densities, whereas bee visitation in mixtures was not significantly influenced at either density. It is possible that facilitation of visitation would change to competition in mixtures at higher densities than the ones used in this study. To determine whether there is a density threshold at which facilitation switches to competition it would be necessary to study a larger range of densities than the two used here.

This is the third field study of pollinator-attracting rust fungi, and the third to suggest facilitation of visitation to co-occurring flowers. The increase in visitation is probably a result of the additional attractiveness of a patch as a result of the fungal contribution

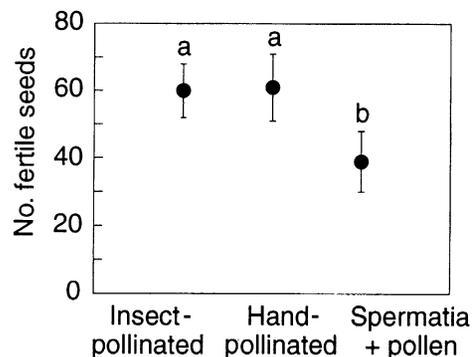


FIG. 5. Mean seed set in flowers with and without fungal spermatia applied to the stigmas at the time of pollination. Flowers were either insect-pollinated (unmanipulated), hand-pollinated with outcross pollen, or "pollinated" with a mixture of spermatia and pollen.

of floral fragrances, floral-like morphology, nectar reward, or a combination of these traits. In an earlier study, I observed pollinator behavior in response to pseudoflowers caused by *P. monoica* on a different species of *Arabis* (*A. drummondii*). In this system, pseudoflowers increase visitation to co-occurring butterflies, which they resemble, by enhancing the attractiveness of the yellow “floral” display, and perhaps also by offering complimentary rewards (Roy 1994b). The other study involves the rust fungus *Uromyces cladii*, which smells like its *Peltandra* host, and attracts the host-specific pollinators, *Elachiptera formosa* (J. Patt, *personal communication*). In this case the rust fungus may facilitate pollination of its host by sustaining a larger pool of pollinators (Patt 1992a, b).

Whether or not increased insect visitation rates lead to increased flowering plant reproduction will depend on the degree of interspecific transfer of pollen and spermatia, and on the numbers of pollinators present. For example, although more insects visited flowers in high-density plots than in low-density plots, there were fewer visits per “flower” in high-density treatments. Thus, even though the high-density treatments had higher insect arrival rates, there were insufficient visitors available in the pollinator pool to “make up” for the increase in “flower” density. Other empirical studies have also found that treatments with higher flower densities often receive more visits overall, but that the increase is not proportional to the increase in flower number (Schmitt 1983, Geber 1985, Sih and Baltus 1987, Schmid-Hempel and Speiser 1988, Bullock and Martiñez del Rio 1989, Klinkhamer et al. 1989). All of these observations are consistent with the prediction that per-“flower” visitation rates should be a nonlinear function similar to a type III functional response. That is, visitation will increase with increasing density until the number of flowers exceeds the number of insects available (saturation), at which point pollination success will decline (Feinsinger 1987, Sih and Baltus 1987).

Competition for visitation can also be described as competition for pollinator preference (Waser 1978a, b, Campbell 1985). The experiments with anemone and pseudoflowers suggest that preference may have more than one component, the combination of which leads to the ultimate outcome of the interaction. For example, although visitors landed more often on anemone, they tended to stay longer per visit on pseudoflowers. If preference is measured by number of visits, then anemone is clearly preferred by most insects since it received 4 times as many visits even when equally common. However, if preference is measured by duration of individual visits, then most insects preferred pseudoflowers. To estimate how much a visit to a pseudoflower might decrease the number of visits to anemone, I divided the average duration per visit to pseudoflowers by that to anemone (from Table 2). For every visit to a pseudoflower, an anthomyiid could have made 3.5

visits to anemone, a muscid could have made 2, a sepsid 1.39, and a “small fly” 3.47. The tendency for insects to stay longer on pseudoflowers is not unique to the anemone–pseudoflower system; I have also noted long visits when pseudoflowers occur with flowers that they resemble (such as buttercups; Roy 1994b).

Although the presence of pseudoflowers sometimes facilitates visitation to anemone, seed set could nonetheless be reduced due to interspecific pollen or spermatia transfer when inconstant foragers move between the species. Halictid bees, which were by far the most common visitors, were relatively inconstant, and in each visit to a pseudoflower about a fifth of their pollen was left behind. These data suggest that interspecific pollen transfer could be a significant factor in reducing seed set of flowers when they co-occur with pseudoflowers. Interspecific pollen transfer may be exacerbated by the length of time that insects spend on pseudoflowers. It seems likely that the longer an insect spends on a pseudoflower, the more of its pollen it will lose since it has been shown in flower pollination studies that long visit times tend to increase pollen deposition (Thomson and Plowright 1980, Galen and Plowright 1985, Thomson 1986, Harder 1990, Mitchell and Waser 1992).

An experiment that examined the effect of spermatia placed on the stigmas of flowers suggested that interspecific movement of insects is likely to result in significant loss of seed set. A similar result has been found when anther smut spores are placed on the stigmas of host flowers (D. Mar, *personal communication*). A possible mechanism for the reduction in seed set is that the plants may be responding to the presence of fungal tissue through localized cell death (a “hypersensitive” resistance reaction), leading to a decrease in the functional area of the stigma and ultimately to loss of seed production. Alternatively, two other mechanisms have been suggested by studies that have measured the effect of interspecific pollen on seed set: allelopathy and clogging of the stigma (Sukada and Jayachandra 1980, Thomson et al. 1981, Kephart 1983, Armbruster and Herzog 1984, Waser and Fugate 1986, Galen and Gregory 1989, Murphy and Aarssen 1989, Randall and Hilu 1990).

The actual effect of the presence of pseudoflowers on the seed set of anemone varied. At Cement Creek seed set was higher in flowers that were adjacent to pseudoflowers, suggesting facilitation. In contrast, at Roadside there was a tendency for seed set to be lower in flowers adjacent to pseudoflowers. Given the complexity of the interactions between pseudoflowers and anemone, a mixed result is not surprising. The data from the visitation experiment suggest that fly visitation to anemone will be facilitated when they occur in mixtures with pseudoflowers. At Cement Creek, seed set was pollinator limited, so facilitation of pollination resulting from pollinator preference for flowers in mixtures could have caused the increase in seed set of

anemone adjacent to pseudoflowers. At Roadside, anemone seed set was not pollinator limited, but competition through interspecific movement could have occurred. In fact, the data suggest that there was more interspecific movement of insects at the Roadside site than at Cement Creek (Bateman's $C = 0.36$ vs. 0.24 , respectively). There were, of course, numerous other differences between the sites that may have contributed to the observed differences. For example, the largest number of visits by bees occurred at Cement Creek, whereas flies and bees were about equally common at Roadside (Table 1). To measure causality more explicitly, future experiments should include measurements of visitor constancy and the prevalence of flies and bees at the time of pollination of the experimental flowers.

The effect of Anemone patens on pseudoflowers

For pseudoflowers, the number and duration of visits per "flower" and the identity of visitors were not significantly influenced by the presence of anemone. However, anemone may still compete for pollinators through improper transfer of spermatia when insects visit anemone flowers after foraging on pseudoflowers, a component of the interaction not measured in this study. Considering that most insects prefer to visit anemone, and that when they move from pseudoflowers they are likely to move to anemone, fungal fitness is likely to be maximized when constancy to the pseudoflowers is higher than observed during this study.

Pseudoflowers may avoid competition by possessing several characteristics that increase the likelihood of fertilization when visitors are rare, similar to some true flowers (Rathcke 1988). For example, pseudoflowers become receptive and attractive to insects 4–8 d earlier at my sites than the first flowers of anemone opened, and individual pseudoflowers can remain receptive for several weeks (Roy 1993). In addition, fungal fertilization was probably not visitor limited, given the relatively high visitation rates recorded in this study (1.58 visits per pseudoflower during 24 h of observation). Even if some interspecific transfer of spermatia reduces the amount of cross fertilization, visitation may be sufficient, particularly since even one visit may effect fertilization. About 20% of the time, more than one fungal mating type is present on a pseudoflower and all that is necessary for fertilization to occur is for an insect to walk around on the pseudoflower (B. A. Roy, unpublished data).

ACKNOWLEDGMENTS

I thank W. Brown, H. Renkin, and H. Winograd for assistance in the field, M. L. Stanton and her lab group for discussion of details both large and small, P. Ward and R. Thorp for verifying insect identifications, and P. Bierzychudek, J. W. Kirchner, R. A. Raguso, N. Waser, and anonymous reviewers for their comments on the manuscript. This research was supported by an NSF Postdoctoral fellowship to B. A. Roy (BSR 9103799).

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