The Effects of Pathogen-Induced Pseudoflowers and Buttercups on Each Other's Insect Visitation

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THE EFFECTS OF PATHOGEN-INDUCED PSEUDOFLOWERS AND BUTTERCUPS ON EACH OTHER'S INSECT VISITATION

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Abstract. Pseudoflowers induced by the rust fungus Puccinia monoica on Arabis spp. are flower-like in color, shape, size, nectar production, and scent. Pseudoflowers attract insects that aid the rust's reproduction in a way that is analogous to pollination in flowering plants. I explored the effects of pathogen-induced pseudoflowers and co-blooming buttercups (Ranunculus inamoenus) on each other's insect visitation by comparing visitation in single-species plots and mixtures. Visitation to pseudoflowers was greater in mixtures containing buttercups than in pseudoflower plots of the same density, and visitation to buttercups was also greater in the mixtures than in pure buttercup plots. Because fungal pseudoflowers and buttercups both appeared to receive greater visitation when associated with each other than when alone, and both species produce food for insect visitors, this interaction could be described as Müllerian floral mimicry. However, several characteristics of this system do not fit standard definitions of mimicry: (1) pseudoflowers are not necessarily mimicking any particular species but instead may be generalized flower-mimics, (2) flower visitors may not always mistake pseudoflowers for flowers but may actually choose them, and (3) under some circumstances pseudoflowers and flowers may compete for visitors. Competition in favor of pseudoflowers is most likely when flies are the primary flower visitors or on the rare occasions when pseudoflowers are common relative to other species.

Key words: Arabis drummondii; competition experiments; facilitation; floral mimicry; fly pollination; Puccinia monoica; Ranunculus inamoenus; rust fungi.

INTRODUCTION

Flower-visiting insects have long been studied for their role in the cross-fertilization of plants. An analogous, but less well-known, phenomenon occurs in some rust fungi where insects effect fertilization by transferring spermatia (gametes) between different mating types on infected plants (Craigie 1927, Buller 1950, Savile 1976, Webber and Gibbs 1989, Roy 1993a). Like flowers, rust fungus spermatia, and the structures that bear them (spermogonia), typically erupt on leaves to form brightly colored patches that exude sugary substances, smell sweet, and attract insects (Buller 1950, Roy 1993a). Moreover, for at least two rust fungi, Puccinia monoica and P. thlaspeos, the similarity to flowers is even more striking because these pathogens induce their hosts (Arabis and other genera in the mustard family) to form flower-like structures (pseudoflowers, Fig. 1) on which the bright yellow fungus produces nectar and scent (Roy 1993a). Because infected Arabis plants are relatively rare, and insect visitation is necessary for sexual reproduction of P. monoica (Roy 1993a), the creation of a flower-like form on the host may benefit the fungus by increasing the probability of insect visitation.

The presence of fungus-induced pseudoflowers in a community may have consequences beyond aiding the sexual reproduction of the pathogen. Because pseudoflowers attract insects that typically visit flowers, they have the potential to affect the pollination of co-occurring true flowers, either negatively by competing for visitors, or positively by attracting more visitors to the area. In previous work (Roy 1993a), I found that insects visited pseudoflowers as often as true flowers, but stayed for much longer durations. Here, I test the hypotheses that pseudoflowers limit the frequency or duration of pollinator visits to co-occurring plants, and conversely that the presence of true flowers increases visitation to pseudoflowers by increasing the effective density of structures that attract insects. Specifically, I ask: (1) Does visitation frequency or duration to pseudoflowers increase or decrease in the presence of true flowers? There are three possible outcomes: decrease in visitation (= competition for visitors), increase in visitation (= facilitation of visitation), and no difference in visitation. If visitation to pseudoflowers increases in mixtures with true flowers relative to pure pseudoflower plots, then it is likely that selection by insects will tend to favor characteristics of pseudoflowers that make them more similar to true flowers. (2) Does visitation to true flowers change as a result of the presence of pseudoflowers? The same potential outcomes enumerated under question one are also possible here. (3) If there are differences in insect attraction between mixtures and pseudoflower plots, are these...
due to plot density or plot diversity? Is it number of “flowers,” or their variety, that most influences insects’ decisions to forage?

**Materials and Methods**

**Natural History**

Pseudoflowers on infected *Arabis drummondii* Gray (Brassicaceae) in western Colorado overlap in flowering time with several co-occurring species including a buttercup (*Ranunculus inamoenus* Greene), a yellow violet (*Viola nutallii* Pursh.), yellow mountain parsley (*Pseudocymopterus montanus* Gray), bluebells (*Mertensia fusiformis* Greene), and white rock-primrose (*Androsace septentrionalis* L.). Here I compare pollinator response to rust pseudoflowers and the buttercup, *R. inamoenus* (Ranunculaceae) because these taxa share the most similar distribution range (Harrington 1954) and had the most overlap in flowering season at my field sites. Pseudoflowers of infected *Arabis* and buttercup flowers are similar in height, diameter, and shape (Fig. 1), and both are bright yellow in the human-visible spectrum (Roy 1993a). Both species are visited by flies and bees, and both produce food for visitors: the yellow, petal-like leaves of pseudoflowers are covered with a sugary solution that also contains spermatia (rust fungus gametes), and the buttercups produce both nectar and pollen (Roy 1993a).

*Arabis drummondii* is a relatively common herbaceous perennial in the montane and alpine meadows of the western USA; it also occurs throughout the northern USA and into Canada (Rollins 1941, Harrington 1954). Many species of *Arabis*, including *A. drummondii*, are susceptible to infection caused by the rust fungus *Puccinia monoica* (Pk.) Arth. (Puccinaceae, Uredinales, Basidiomycetes) (Anonymous 1960, Arthur 1962, Farr et al. 1989, Roy 1993b). Infection of *A. drummondii* at my sites occurs in the late summer from wind-borne basidiospores produced on the primary host, the grass *Trisetum spicatum* (L.) Richter. Infection is systemic; over the fall and winter the fungus grows within the host, invading the meristem and affecting future growth. Infected *Arabis* plants produce one to several flower-like infected rosettes (pseudoflowers) in the spring, but rarely produce true flowers (Roy 1993a). The reproductive structures of the rust fungus form on the surface of the pseudoflowers; insects are required to transfer spermatia to receptive hyphae belonging to a different mating type (Roy 1993a).

Visitation rate is a useful index of reproductive success for the rust *P. monoica*. Insect exclusion experiments show that visitation is necessary for rust reproduction, and that multiple visits may increase the likelihood of sexual spore formation (Roy 1993a). It is not known how insect visitation affects seed set in *R. inamoenus*, although insect visitation increases seed set in another alpine buttercup, *R. adoneus* (Stanton and Galen 1989). Like *R. adoneus*, *R. inamoenus* is often pollinated by flies. In general, multiple visits by flies are usually necessary for full seed set and pollen removal (Kearns 1990).

**Experimental Design**

I measured insect visitation in artificial arrays in a montane meadow in Rustler’s Gulch at ≈2960 m elevation, ≈4 km north of the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. I prepared the site on 29 May by removing all flowers from four 80 x 100 cm treatment plots, spaced 5 m apart along a linear transect. In these plots I arranged freshly picked flowers and pseudoflowers in rectangular treatment arrays of florists’ pics (small plastic vases). Flowers and pseudoflowers were replaced daily and wilted ones were replaced immediately. Artificial arrays were used rather than intact plants to allow control over the spatial arrangement of plants.

The experiment included four treatments: (1) high density pseudoflowers, (2) low density pseudoflowers, (3) high density buttercups, and (4) a high density mixture composed of 50% pseudoflowers and 50% buttercups in a “checkerboard” array. The high density treatments contained 20 pseudoflowers or flowers per 0.8-m² plot (25/in²), and low density treatments contained 10 pseudoflowers or flowers per plot (12.5/in²). Pseudoflower density in the meadow was 0.5/in² and buttercup density was 1.5/in², but total flower density was 60/in². Because studies near the study site found that insect visitation rates may depend on total flower density, rather than density of a particular species (Thomson 1981, 1982), I chose treatment densities that...
were a compromise between the buttercup/pseudo-
flower densities and total flower density. Relatively
high densities were also required to ensure measurable
visitation, since visitation rates can be low at montane
Insect visits to each of the four kinds of treatment
plots were tallied for 14 20-min observation periods.
To eliminate observer bias, two observers were ran-
domly assigned to treatment plots for one 20-min ob-
servation period, then randomly assigned among the
remaining two treatments for another observation pe-
riod. Each pair of observation periods therefore con-
stitutes a replicate during which visitation to each of
the four treatments was tallied once. The number of
replicates observed varied among days depending on
weather (range: 2–5 replicates). To remove bias due to
plot position, the order of the treatment plots along
the transect was rearranged after each complete set of
four (i.e., after each replicate) had been observed. Ob-
servations were made between 1000 and 1500, under
clear to partly cloudy skies, on four different days (29
and 31 May, and 1 and 3 June 1992).
In addition to numbers of visits, duration of each
insect visit was measured. Insects were timed only when
they were within the sexual parts of buttercup flowers,
including the nectaries, and when they were on the
fungal-covered portions of pseudoflowers. Intervals of
obvious basking or resting on either species were not
included in visitation times.

Analysis
To determine whether or not visitation patterns were
similar among days of the experiment, I used a bal-
anced design, mixed-model. Type III sums of squares,
two-way factorial ANOVA, with treatment as a fixed
factor and date as a random factor. Number of visits
and visit duration were square-root transformed prior
to analysis to obtain normality and homogeneity of
variance. For a posteriori comparisons among means
I used Tukey HSD tests (Sokal and Rohlf 1981, Kirk
1982). All analysis used the statistical program JMP,

To determine whether differences in visitation to
pseudoflowers alone vs. pseudoflowers in mixtures were
attributable to differences in plot density or diversity,
I used two orthogonal a priori contrasts: (1) I asked
how important plot density was in influencing visitors
to forage by contrasting visits per plant in low density
pseudoflower plots against the high density plots (an
average of the mixture and the high density pseudo-
flower plots) and, (2) I asked how important plot di-
versity was by contrasting visitation to the high density
pseudoflower plots with that to the high density
mixtures. Note that contrast 2 asks whether there is a
difference in visitation when pseudoflowers are sur-
rounded by different neighbors (high density mixture)
vs. the same neighbors (high density pure pseudoflow-
er).

My ability to assess the effects of the pseudoflowers
on buttercup visitation was limited by the lack of a low
density buttercup treatment. However, with the four
treatments I could ask whether buttercups receive more
visits per flower in the mixture than in single-species
treatments of equivalent total flower density (i.e., high
density treatments), and I could measure both density
and diversity effects on visitation to pseudoflowers.

RESULTS
Flower visitors
Anthomyid flies were the primary visitors to both
pseudoflowers and buttercups (Table 1), and the same
individuals were observed to move between the two
species. In mixtures, 17% of insect visitors leaving but-
tercups moved to another “flower” within the same
plot, and 70% of these changes were from buttercups
to pseudoflowers. No visitors leaving pseudoflowers
moved to buttercups in the same mixtures. However,
it was difficult to estimate the flower constancy of vis-
itors to pseudoflowers during the 20-min observation
times, because visitors tended to stay longer on pseu-
doflowers (range = 1 s–16.93 min, mean = 2.15 min,
\( n = 248 \)) than on buttercups (range = 1 s–4.16 min,
mean = 0.76 min, \( n = 131 \)). Thus, fewer flower-to-
flower changes were likely to be observed if the insect

<p>| Table 1. Visitors of pseudoflowers on infected Arabis and of the flowers of the buttercup Ranunculus inamoenus (number of each visitor type and percent of total visits). |
|-----------------------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th>Plant species</th>
<th>Total visits</th>
<th>Anthomyid flies</th>
<th>Anthomyid flies</th>
<th>Calliphorid flies</th>
<th>Scathophagid flies</th>
<th>Unidentified flies</th>
<th>Halictid bees</th>
<th>Unidentified visitors</th>
</tr>
</thead>
</table>
| Arabis drummondii  
(pseudoflowers) | 248 | 69 | 28 | 109 | 44 | 3 | 1 | 19 | 8 | 32 | 13 | 0 | 16 | 6 |
| Ranunculus inamoenus  
(flowers) | 131 | 40 | 30 | 71 | 54 | 0 | 1 | 1 | 9 | 7 | 9 | 7 | 1 | 1 |
| * Flies in the ?Anthomyid category were probably Anthomyids, but this category reflects the uncertainty of rapid identifi-
cations.  
† Scathophagid flies ambush prey from flowers, and were observed doing so during this experiment from infected Arabis rosettes.  
‡ Individual infected rosettes (pseudoflowers) were considered to be analogues of one flower (see Fig. 1).
first visited a pseudoflower; alternatively, the insects might have been showing a preference for pseudoflowers.

Foraging bouts were approximately the same length in all plot types (mean number of "flowers" visited per insect in low density pseudoflower plots = 1.02, in high density pseudoflower plots = 1.09, in high density but- 
cercups = 1.07, and in the high density mixtures 
in all plot types (mean number of "flowers" visited per 

Effects of the presence of buttercups on visitation to pseudoflowers
The presence of buttercups increased visitation to 
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Effects of plant density on visitation
Visitation to plots containing pseudoflowers was 
density dependent. In all 14 replicate observation pe-
riods, total visitation per plot was higher in the high 
density plots (Table 2, number of visits per plot) and 
this difference was significant (P = .02). There was also 
a significant increase on a per pseudoflower basis (Ta-
ble 2, number of visits per pseudoflower, a priori con-
trast \( F = 4.01, df = 1, 36, P = .05 \)). 

Associated with the differences in visitation number 
 between high and low density treatments, there were 
significant differences in visit duration among treat-
ments, with low density pseudoflower treatments re-
ceiving significantly less total visitation time than high 
density treatments (Table 2, time per plot). However, 
duration of individual visits to pseudoflowers was not 
affected by density (Table 2, time per pseudoflower).

Effects of observing visitation on different days
Pollinator activity varied significantly among the days 
on which observations were made (Table 3). On the 
final day there were fewer visits and the insects stayed 
less long, probably as a result of cooler temperatures. 
There was no significant interaction of date and treat-
ment for visits per plot (\( F = 1.28, df = 9, 40, P = .28 \)), 
visits per pseudoflower (\( F = 1.21, df = 6, 30, P = .32 \)), 
visits per buttercup (\( F = 1.47, df = 3, 20, P = .25 \)), or 
time per plot (\( F = 1.20, df = 9, 40, P = .32 \)) indicating 
that the basic visitation patterns remained constant 
even though there were fewer visitors over time.

Discussion
Potential reasons for the observed effects on visitation
Pseudoflowers and buttercups received significantly 
more visitation in mixtures than in pure stands (Table 
2), and this pattern was consistent for all 4 d of the 
experiment (indicated by the lack of a significant in-
teraction between date and treatment). Why are pseudoflower/buttercup mixtures more effective in attracting insects? There are at least three possible reasons: (1) increased floral display through an increase in apparent density, (2) complementary attraction cues, and (3) complementary pollinator rewards. In this system there is potential for all of these factors to be operating.

The increase in visitation to pseudoflowers in the mixtures over low density pure pseudoflower plots was partly, but not entirely, due to an increase in overall plot density. The high density mixtures and the high density pseudoflower plots had the same overall density of “flowers.” If the increase in visitation to pseudoflowers in the mixture over that in low density pure plots was the result of an increase in overall density, then visitation per pseudoflower in the pure high density plots should be about the same as that in the high density mixtures, as is the case (Table 2). Nevertheless, a closer look at the data suggests that diversity may also be influencing visitation since the mixture received somewhat more visitation than the high density plot (Table 2).

Complementation (Rathcke 1983) is a mechanism, in combination with density, that may help explain the synergistic effect of a mixture on pollinators. Complementary attraction may occur in mixtures because there are differences between pseudoflowers and buttercups that appeal to different visitors, thus leading to greater visitation overall. For example, buttercups reflect in the ultraviolet range, whereas pseudoflowers do not (Roy 1993a), and pseudoflowers have a strong sweet scent, whereas buttercups do not (B. A. Roy, personal observation). Resource complementarity is also possible since the flowers of *Ranunculus inamoenis* have abundant pollen but little nectar, whereas pseudoflowers have abundant nectar but no pollen (Roy 1993a).

The increase in visitation to mixtures beyond what can be attributed to density effects is small (Table 2), and the reasons behind this increase are likely to be difficult to detect in small plots receiving few visitors. Nonetheless, it is worth examining the data to see whether a mechanism can be differentiated. Visitation to “flowers” in the mixtures could be greater for three different reasons: (1) more visitors are attracted, (2) the same visitors make more return trips, or (3) individual visitors make more visits within a plot before leaving. I cannot differentiate between (1) and (2), but I have data that bears on the third possibility. If foraging bouts length (number of “flowers” visited per individual visitor) is contributing to the increased number of visits in mixtures, then insects should visit more “flowers” per plot in mixtures vs. pure stands of equivalent density. By this measure the means show no evidence of increased visitation per insect in mixtures for any treatment (high density pseudoflower = 1.09, high density buttercup = 1.07, high density mixture = 1.07 visits per insect per treatment), suggesting instead that there may be more insects attracted overall or that they return more frequently.

### A case of Müllerian mimicry?

Because insect visitation to both pseudoflowers and buttercups increased when they were associated, and both species offer rewards for pollinators, and they were visited by the same flower visitors, this interaction could be considered an example of Müllerian floral mimicry. In Müllerian floral mimicry “two or more species offer food rewards, convergence in floral characters, and share the same pollinator” (Dafni 1986:82-83). The increase in visitation to mixtures of flowers is presumably due to a density or frequency-dependent increase in display attractiveness to pollinators (Macior 1971, Proctor and Yeo 1972, Little 1983, Thomson 1983, Dafni 1984, 1986). Müllerian floral mimicry differs from the more commonly studied Batesian floral mimicry, in which the mimic produces no reward for pollinators and relies on its similarity to a rewarding model to attract pollinators (reviewed in Little 1983, Dafni 1984, 1986). Some authors prefer the term Müllerian convergence to Müllerian mimicry because they reason that rewarding flowers that resemble one another are simply examples of convergent evolution resulting from a generalized response to insect pollination (Wickler 1968, Wiens 1978).

I suspect that the fungal pseudoflowers are not mimicking any particular species, but are more generalized flower mimics, taking advantage of insects that visit not only buttercups but also other co-blooming species visited by generalist pollinators. The concept of a more generalized mimicry could fit within the notion of Müllerian mimicry, which often involves numerous species that share generalist pollinators (“mimicry rings”) (Vane-Wright 1976, Little 1983, Dafni 1984, 1986). Many of the flowers that co-occur with pseudoflowers are also visited by generalist pollinators such as flies, and many are also yellow in color. Additional evidence

<table>
<thead>
<tr>
<th>Time/plot (s)</th>
<th>914.9 ± 199.40a</th>
<th>901.9 ± 196.44a</th>
<th>800.6 ± 149.85a</th>
<th>240.3 ± 75.20b</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. visits/buttercup</td>
<td>0.21 ± 0.09a</td>
<td>0.23 ± 0.09b</td>
<td>0.20 ± 0.07a</td>
<td>0.05 ± 0.03b</td>
</tr>
<tr>
<td>No. visits/pseudoflower</td>
<td>0.40 ± 0.10a</td>
<td>0.36 ± 0.11a</td>
<td>0.38 ± 0.09a</td>
<td>0.22 ± 0.05a</td>
</tr>
<tr>
<td>No. visits/plot</td>
<td>7.92 ± 1.80a</td>
<td>8.38 ± 1.21a</td>
<td>8.95 ± 1.44a</td>
<td>3.56 ± 0.70a</td>
</tr>
<tr>
<td>29 May</td>
<td>31 May</td>
<td>1 June</td>
<td>3 June</td>
<td></td>
</tr>
</tbody>
</table>

Different superscript letters following the means within a row indicate significant ($P < .05$) differences among means (Tukey HSD tests).
of a more generalized mimicry is also suggested by the fact that pseudoflowers have numerous flower-like characteristics (Roy 1993a) that are similar but not identical to any particular co-occurring flower, and by the fact that visitation to pseudoflowers can also be greater in experimental mixtures including non-yellow flowers such as Pulsatilla patens (Ranunculaceae), which has large yellow anthers and nectaries but blue petals, and Claytonia lanceolata (Portulacaceae), which is pink (B. A. Roy, unpublished data).

Factors that may modify the apparent mutualistic relationship between buttercups and pseudoflowers

Although both pseudoflowers and buttercups appear to benefit from their association, pseudoflowers may be preferred by flower visitors. This is suggested by several factors: (1) pseudoflowers received more visits than buttercups in the mixtures (Table 2), (2) pseudoflowers received more visits in pure pseudoflower high density plots than buttercups did in their pure high density plots (Table 2), (3) pollinators spent substantially more time on pseudoflowers than on buttercups (Table 2), and (4) pollinators were never observed moving from pseudoflowers to buttercups. Preference indicates a kind of directed behavior that is contrary to what some people (e.g., Wickler 1968, Wiens 1978) consider an important element of floral mimicry: insects confusing one flower for another. It is possible that the directed behavior seen in this experiment was an artifact of the design since infected plants were more clustered in experimental plots than they usually are in a meadow. In other words, under normal circumstances, infected plants may be rare enough that it is hard for insects to specialize on them and they rely on occasional chance visits. On the other hand, preference and specialization may occur and could be aided by the strong sweet odor emitted by pseudoflowers.

Given that the most common visitors, anthomyid flies, seemed to prefer pseudoflowers there is potential for direct pollinator competition, with the buttercups on the losing side. There was no evidence of direct competition during this experiment since buttercups received more visits when adjacent to pseudoflowers than they did in pure stands (Table 2). However, if insects do prefer pseudoflowers, a benefit for buttercups may not always be realized when they occur together. For example, indirect competition, by means of improper pollen transfer to pseudoflowers, which have sticky surfaces that trap pollen (B. A. Roy, personal observation), could lead to decreased buttercup pollination. Since all insects that changed to a different species when in a mixture moved from buttercups to pseudoflowers, pollen loss was likely. Further experimentation is necessary to determine the degree of pollen loss and the consequences for buttercups.

Vane-Wright (1976) recognized that most examples of Müllerian floral mimicry would also contain an element of competition for pollination. He suggested that these cases be called “antergic inviting mimicry,” which he defined as occurring when “…the mimic simulates a signal of positive interest to the operator, as a result of which the model loses in some way. The mimic is always of some potential value to the operator” (Vane-Wright 1976:38). By suggesting this new terminology, Vane-Wright also recognized the inherent differences between plant and animal mimicry. Most animal mimicry is a device to avoid predation and is thus “warning” in nature, whereas floral mimicry is “inviting.” Because animals are being invited in, not warned away, there is always some potential for competition for their services.

Floral mimicry may not be evolutionarily stable because it is so easy for competition to occur in pollination systems. Indeed, there are few documented cases of floral mimicry compared to animal mimicry (Williamson 1982), and very few of these fall into the “Müllerian” category (for examples see Brown and Kodric-Brown 1979, Schemske 1981, and Thomson 1981). There are several reasons why the rarity of infected plants may be an important factor contributing to the evolution of this particular system. First, rarity will increase the probability that insects will “mistake” pseudoflowers for true flowers since they will have little opportunity to learn to differentiate them from true flowers (Williamson 1982). Second, the rarity of infected plants minimizes the potential for dramatic pollen loss due to improper transfer, making it more likely that the benefits of sharing generalist pollinators for true flowers (more visitors) may outweigh the potential costs (pollen dilution). And third, if infected plants are too rare to attract sufficient visitors on their own for reproduction, then rarity will serve to increase the rate of selection towards convergence (Fisher 1930). Selection favoring convergence to a flower-like form should be even stronger if pollinators are scarce, which is likely in this system because (1) the plants occur at high altitudes, where insects are less common, and (2) infected Arabis is receptive shortly after snow melt when few flower-visiting insects are available.

Conclusions

Pseudoflowers and buttercups influence each other’s visitation and this interaction can be complex. Pseudoflower rarity, an obligately outcrossing mating system for the fungus, and increased visitation in the presence of flowers all favor pseudoflower convergence to a flower-like form. Selection for similarity of flowers to pseudoflowers may also occur when visitation and fitness increase as a result of the similarity, but not when competition occurs. Insect presence and abundance, and thus selection, varies strongly among years and probably among sites. For example, in 1990 at the same site as the study described herein, halictid bees, which forage primarily on pollen, were more common than flies, and 74% of all visits to buttercups were by
bees (B. A. Roy 1993a, unpublished data). By contrast, in 1992, flies were more common, and halictid bees only accounted for 9% of all visits to buttercups. Under 1990 conditions, neither competition nor facilitation between buttercups and pseudoflowers was possible since they did not share insect visitors. Under 1992 conditions, either a mutualistic or competitive relationship was possible, depending on the net fitness effects of visitation, because they did share visitors. Long-term or multiple-site studies that quantify visitation and fitness consequences are necessary to elucidate common insect patterns, the relative strength of selection for convergence vs. competition, and causes for the season-to-season or site-to-site variance in insect abundance and behavior.

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LITERATURE CITED


