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## Effects of low-efficiency pollinators on plant fitness and floral trait evolution in *Campanula americana* (Campanulaceae)

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**Abstract** Floral visitors vary in their pollination efficiency and their preferences for floral traits. If low-efficiency pollinators decrease the amount of pollen available to higher efficiency visitors, then low-efficiency visitors may actually have negative fitness consequences for the plants that they visit. We used experimental arrays in two populations to determine the floral preferences and the fitness effects of low-efficiency (or “ugly”) pollinators on *Campanula americana*. These ugly pollinators (halictid bees) preferentially visited flowers with pollen over flowers that had had their pollen removed. *C. americana* pollen color varies quantitatively from light tan to dark purple, and we found that natural variation in pollen color influenced the magnitude of halictid preferences for flowers with pollen. In general, preferences for flowers with pollen were stronger when the ugly pollinators foraged in arrays of flowers with tan-colored pollen than in arrays with purple-colored pollen. When plants received few visits by efficient *Bombus* pollinators, visits by ugly pollinators significantly decreased siring success relative to plants where visits by ugly pollinators were prevented. In contrast, ugly pollinators did not influence siring success when higher efficiency pollinators were more abundant. Thus, the relationship between low-efficiency pollinators and the plants that they visit varies from commensalistic to antagonistic depending on the presence of other pollinators in the community. Our findings suggest that the negative fitness effects and floral preferences of low-efficiency or “ugly” pollinators may contribute to the maintenance of a pollen color polymorphism in *C. americana*.

**Keywords** *Campanula americana* · Low-efficiency pollinators · Plant–insect interactions · Pollen robbing · Pollen color

### Introduction

Pollinators often exert strong selective pressures on floral traits. In many systems increased pollinator visitation rates translate directly into increased male and female plant fitness (Eckhart 1991). However, plants may be visited by multiple types of pollinators that vary in efficiency, and the low-efficiency visitors do not always transfer pollen effectively (Schemske and Horvitz 1984; Fishbein and Venable 1996). While many studies have shown how efficient pollinators affect plant fitness and drive selection on floral traits (e.g., Galen 1996), the effects of low-efficiency pollinators on plant fitness and floral trait evolution have been relatively ignored (but see Stanton et al. 1991; Mazer and Meade 2000).

Pollinator efficiency may be defined as “the amount of pollen deposited on a receptive...stigma relative to the vector pollen load,” (“vector pollinating efficiency,” Inouye et al. 1994). As such, pollinator efficiency can vary for a variety of reasons including pollen consumption, pollen transfer effectiveness, and preference for specific floral morphs. Extremely inefficient pollinators have been dubbed “ugly” pollinators (Thomson and Thomson 1992; see also “pollen robbers” Inouye 1980) because of their tendency to consume copious amounts of pollen while transferring little pollen to female reproductive structures. These ugly pollinators can decrease the male component of plant fitness by limiting the amount of pollen available to more efficient pollinators. Observational studies suggest that such fitness consequences are possible in natural systems (Stanton et al. 1991).

If ugly pollinators have large fitness effects and respond to variation in floral traits, then ugly pollinators may play a significant role in floral trait evolution by virtue of their negative effects on plant fitness. The fitness effects of such pollinators may vary with the component community of

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pollinators. For example, if both efficient and inefficient pollinators are present in large numbers, the abundance of efficient pollinators may swamp out the negative fitness effects of the inefficient pollinators. If inefficient pollinators outnumber efficient pollinators, then the negative effects of inefficient pollinators may dominate. Alternatively, when efficient pollinators are rare, even the small quantities of pollen transferred by inefficient pollinators may enhance reproductive success. Thus, variation in pollinator community composition and the interactions among pollinators could produce geographical or temporal variation in selective forces that can maintain variation in floral traits (Stanton et al. 1991; Mazer and Meade 2000; Fenster and Dudash 2001).

We use *Campanula americana*, a woodland herb, to investigate the role of inefficient pollinators in floral trait evolution. Several small solitary bee species (Halictidae) commonly visit *C. americana*. These halictid visitors are considered “ugly” or inefficient pollinators because they preferentially visit and consume the pollen of male-phase flowers while avoiding female-phase flowers (Johnson et al. 1995). Our study addresses four questions: (1) do halictids use pollen presence as a visitation stimulus? (2) does pollen color, a floral trait, affect halictid visitation rates? (3) do halictids affect plant siring success? and (4) if so, does the abundance of efficient pollinators alter the effects of halictids on plant siring success?

## Materials and methods

### Natural history of the study system

*Campanula americana* (*Campanulastrum americana*, Campanulaceae), the tall bellflower, is a woodland herb endemic to North America. Flowers of *C. americana* are protandrous, opening in male phase. This species, along with other members of the genus *Campanula*, has a secondary pollen presentation mechanism in which pollen is deposited on pollen-collecting hairs on the outer surface of the style prior to anthesis. Pollen becomes available to pollinators as the pollen-collecting hairs retract over time and with mechanical stimulation from pollinator activity (Nyman 1993). Most pollen is removed within 4 h of anthesis (Evanhoe and Galloway 2002), and flowers are then effectively neuter until the next day when the opening of the stigmatic lobes indicates the onset of female phase. The presence or absence of pollen can be easily assessed visually.

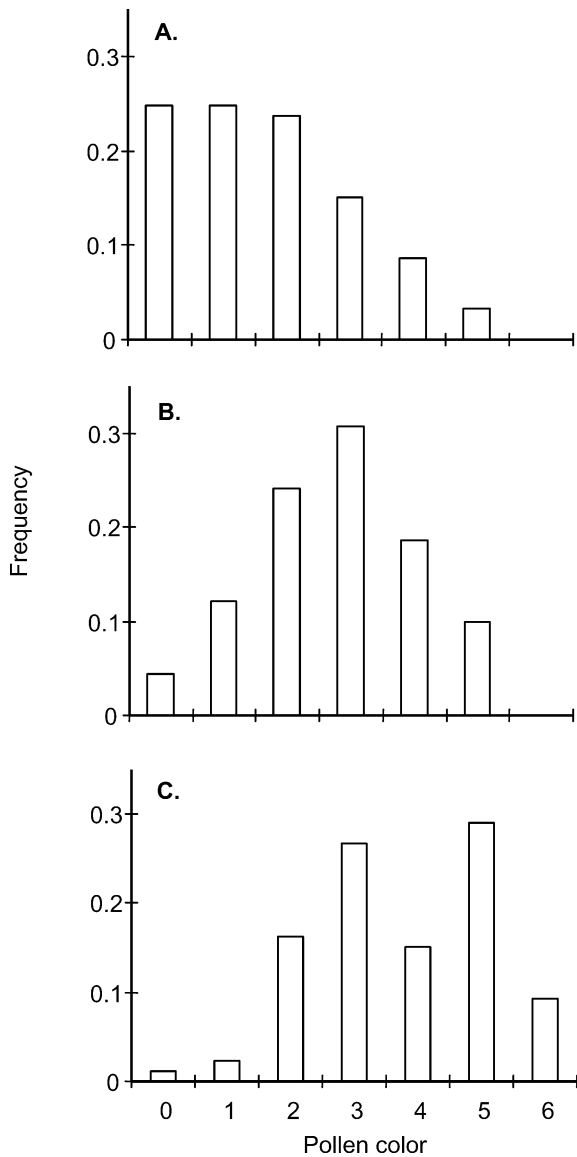
Pollen color in *C. americana* varies quantitatively from deep purple to light tan among plants, but is relatively constant across flowers of a single plant (J. Lau, personal observation). The color can be scored by comparison to Southern Accent brand paint sample 302A which ranges from almost white (assigned a value of zero) to deep purple (assigned a value of six). We evaluated the distribution of pollen color in three populations in southwestern Virginia by scoring approximately 90 randomly selected individuals in each population

(Fig. 1). We selected the two populations that differed most in pollen color frequency and pollinator communities for detailed study. The Mountain population located under the forest canopy near the top of Salt Pond Mountain (Pembroke, Va., USA latitude 37.36, longitude  $-80.55$ ), consisted predominately of plants with dark purple pollen (Mean=3.72, SD=1.38,  $n=86$ ). It had relatively low pollinator visitation rates ( $1.09 \pm 0.14$  visits/min, SE) and was predominately visited by halictids; bumblebees (*Bombus* spp., including *B. vagans*, *B. bimaculatus*, and *B. affinis*) accounted for 7% and halictids 93% of observed visits. No megachilid visitors (leaf cutting bees) were seen. The River population located 9 km away and 655 m lower in elevation (latitude 37.28, longitude  $-80.62$ ) consisted largely of plants with tan-colored pollen (Mean=1.66, SD=1.27,  $n=93$ ). It had higher visitation rates ( $1.74 \pm 0.12$  visits/min, SE) and was visited regularly by *Bombus* (17%), megachilids (36%), and halictids (47%).

### Pollinator preferences

Pollinators may use male reproductive characters as floral cues (Solomon 1987; Ashman 2000). To determine whether any of the pollinators in this system exhibited preference for either pollen color or pollen presence, we observed pollinator visits to experimental floral arrays. Each array consisted of seven or eight flower stalks placed in a hexagonal pattern with every stalk 15 cm away from its nearest neighbors. Flower stalks were collected each morning or the previous day and trimmed just prior to use so that only one male-phase flower remained.

To determine whether pollinators respond to the presence of pollen, three or four of the randomly located flowers had pollen present and three or four flowers had no pollen. Flowers without pollen either had their pollen removed by pollinators in previous arrays or, more commonly, had their pollen gently rubbed off by the observer. Flowers with pollen were scored for pollen color to determine whether pollen color influences the preference of visitors for flowers with pollen. The arrays were categorized by the pollen color of the flowers with pollen. Tan arrays were those arrays where all flowers received pollen color scores of two or less; purple arrays were those arrays where all flowers received pollen color scores of four or greater, and mixed arrays were those arrays that contained a mixture of flowers with tan-colored pollen and flowers with purple-colored pollen. Each array was then observed until 25 pollinator visits had been made to the flowers. A visit was recorded only if the insect actually landed on the open face of the flower. For each visit, insect and flower identities were recorded. If over 50% of the pollen was removed from a flower during the observation period, the flower was replaced with another one of similar pollen color. The arrays were conducted during the peak blooming season. In the River population, 19 arrays (4 tan, 12 mixed color, and 3 purple) were observed over 11 days. In the Mountain population, 15 arrays (6 tan and 9 purple) were observed over 6 days; 959 visits were recorded.



**Fig. 1a–c** Pollen color distribution of three populations of *C. americana* near Salt Pond Mountain. Pollen color ranged from near-white (0) to deep purple (6). **a** “River population,” 488 m elevation; **b** “Cave population,” 700 m elevation; **c** “Mountain population,” 1,143 m elevation

The influence of pollen presence on the number of visits received was analyzed with ANOVA. The model included pollen presence, type of visitor (*Bombus*, halictid, or megachilid), array color, and all interactions as fixed effects. Array, nested in array color, was included in the model as a random blocking factor, and its type III mean square was used as the error term for tests involving array color. The populations were analyzed separately because they differ in pollinator fauna and no mixed color arrays were conducted in the Mountain population. The response variable was number of visits by each visitor to each type of flower (pollen, no pollen) in each array. Because we were testing for differences in visitation rates of the various pollinators to flowers with pollen versus flowers without pollen, the main effects of array color and visitor

are not of interest. To account for the unbalanced design when only seven flowers were used in the array, we weighted the number of visits to flowers of each treatment; the number of visits to flowers in the treatment represented by three stems was multiplied by 1.33. Since analyses were conducted on array totals, this effectively equalized the treatments. Because of the significant ( $P < 0.0396$ ) three-way interaction term of visitor  $\times$  pollen  $\times$  array color in the Mountain population, additional analyses focusing on the response of each type of pollinator to pollen presence and array color were performed. Additionally, one-way ANOVAs testing for pollen preferences within each array color were conducted in order to interpret significant interactions, and these results are reported in the text. In all analyses, zeros resulting from a specific visitor not visiting the array were not included in the analysis; zeros resulting from a specific visitor visiting the array, but not visiting both pollen treatments, were included in the analysis.

#### Fitness effects of halictids

To determine the fitness consequences of ugly pollinator visitation, we estimated siring success in experimental arrays where we manipulated the number of *Bombus* and halictid visits. We constructed arrays of genotypically distinct plants at the Mountain Lake Biological Station, Pembroke, Va., USA. Each array consisted of six experimental plants, each with five flowers: four plants had only female-phase flowers, and two plants had only male-phase flowers. The two “male” plants were the only potential sires in the area (the nearest known *C. americana* population was approximately 3.5 km away). We randomly selected one of the two males to receive halictid visitors (halictids present treatment), while we prevented halictids from visiting the second male plant by waving away any approaching halictid bees and by physically removing any halictids that successfully landed on open flowers (halictids absent treatment). All plants were exposed to pollinators until each of the focal males had received the same number of *Bombus* visits. Two *Bombus* visitation treatments were applied; for 11 arrays, both focal male plants received 6 *Bombus* visits (low *Bombus* visitation treatment); for the other 11 arrays, both focal males received 30 *Bombus* visits (high *Bombus* visitation treatment). Once a male had received the prescribed number of *Bombus* visits, further visitation by *Bombus* was prevented. The number of halictid visits was recorded.

Plants used in this experiment were first screened to determine their allelotypes at two loci (PGI and PGM) using starch gel electrophoresis (Werth 1985). Plants in each array were selected so that all sire/dam pairs produced offspring of distinct allelotypes so that we could trace each offspring to only one of the sires. Twenty-two arrays were tested over 20 days during the peak flowering season. We then collected each fruit produced by the female test flowers, germinated the seeds, and genotyped representative offspring to determine sire

identity. Sires for 167 offspring from 76 fruits in the low pollinator treatment and 161 offspring from 63 fruits in the high pollinator treatment were identified.

We used logistic regression to determine how the number of halictid visits affected the relative siring success of plants receiving halictid visitors. *Bombus* visitation treatment (dichotomous explanatory variable), number of halictid visits (continuous explanatory variable), and the interaction were included in the model. The response variable was number of seeds sired by the plant receiving halictid visitors over the total number of sampled seeds. Each array was an independent observation. Because of the significant interaction between *Bombus* visitation treatment and number of halictid visits ( $P=0.0021$ ), separate analyses were performed for each *Bombus* visitation treatment.

The effects of the halictid treatment (presence or absence) and interactions between the halictid treatment and the *Bombus* visitation treatment (low vs high) on siring success were analyzed with  $G$ -tests assuming the null hypothesis of equal siring success. These analyses were performed on the total number of seeds sired combined across all arrays in a particular *Bombus* visitation treatment. An initial two-way analysis found a significant interaction between *Bombus* visitation treatment and halictid treatment on siring success; therefore, separate  $G$ -tests were performed for each *Bombus* visitation treatment.

## Results

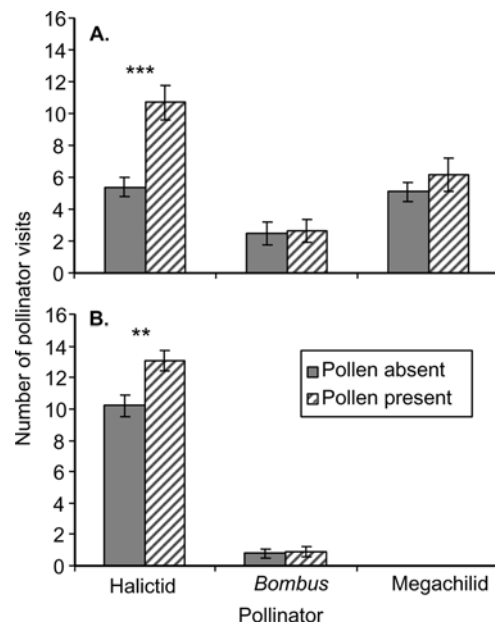
Do pollen presence and color influence pollinator visitation rates?

Pollinators preferentially visited flowers with pollen over those without pollen (Table 1). This effect was driven entirely by the selectivity of the halictid visitors (Table 1 visitor  $\times$  pollen; Fig. 2). Overall, halictids visited flowers with pollen 36% more frequently than flowers without pollen (River  $F_{1,15}=22.28$ ,  $P=0.0003$ ; Mountain  $F_{1,13}=8.40$ ,  $P=0.0124$ ), whereas *Bombus* and megachilid visitors showed no preference for pollen presence (*Bombus* River  $F_{1,7}=0.03$ ,  $P=0.86$ ; *Bombus* Mountain  $F_{1,6}=0.00$ ,  $P=0.96$ ; megachilid River  $F_{1,12}=0.00$ ,  $P=0.99$ ). Halictids were the most common visitors to arrays in both the Mountain and River populations (Fig. 2).

Visitors differed in their response to pollen presence and pollen color in the Mountain population (Table 1), therefore we analyzed patterns of visitation of halictids and *Bombus* separately in that population. Pollen presence did not significantly influence the number of visits from *Bombus* pollinators in any array color (results not shown). In contrast, in this population, halictids' selectivity for flowers with pollen depended on pollen color (pollen  $\times$  array color Table 2). Halictids preferred flowers with pollen when flowers had tan-colored pollen ( $F_{1,5}=11.76$ ,  $P=0.0187$ ; Fig. 3), but there was no significant difference between the number of halictid visits to flowers with or

**Table 1** ANOVA of the effect of pollen presence and pollen color on the number of pollinator visits to flowers in experimental arrays in two populations of *C. americana*. Type III MS for array (array color) was used as the error term for tests including array color

Source	df	MS	F	P
<b>River population</b>				
Visitor	2	58.31	5.26	0.0083
Pollen	1	41.55	3.75	0.0584
Array color	2	32.72	1.99	0.1697
Visitor $\times$ pollen	2	49.35	4.45	<b>0.0165</b>
Visitor $\times$ array color	4	40.74	2.47	0.0864
Pollen $\times$ array color	2	1.67	0.10	0.9044
Visitor $\times$ pollen $\times$ array color	4	2.22	0.13	0.9672
Array (array color)	16	16.48	1.49	0.1411
Error	52	11.09		
<b>Mountain population</b>				
Visitor	1	651.78	109.47	<0.0001
Pollen	1	27.49	4.62	<b>0.0415</b>
Array color	1	3.89	3.70	0.0768
Visitor $\times$ pollen	1	28.23	4.74	<b>0.0391</b>
Visitor $\times$ array color	1	0.24	0.23	0.6431
Pollen $\times$ array color	1	29.35	27.87	<b>0.0001</b>
Visitor $\times$ pollen $\times$ array color	1	5.51	5.23	<b>0.0396</b>
Array (array color)	13	1.05	0.18	0.9989
Error	25	5.95		

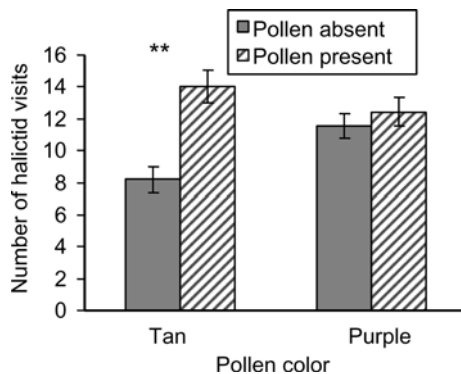


**Fig. 2a, b** Means  $\pm$  SE for the number of visits to *C. americana* flowers with pollen versus flowers without pollen in experimental arrays. The arrays were located in the River (a) and Mountain (b) populations. Asterisks indicate significant tests for the effect of pollen presence for each visitor type (\*\* $P<0.01$ , \*\*\* $P<0.001$ )

without pollen in arrays consisting of flowers with purple-colored pollen ( $F_{1,8}=0.35$ ,  $P=0.57$ ; Fig. 3).

**Table 2** ANOVA of the effect of pollen presence and pollen color on the number of halictid visits to flowers in experimental arrays in the Mountain *C. americana* population. Type III MS for array (array color) was used as the error term for tests including array color

Source	df	MS	F	P
Pollen	1	81.34	8.40	<b>0.0124</b>
Array color	1	5.81	3.23	0.0957
Pollen×array color	1	44.01	24.45	<b>0.0003</b>
Array (array color)	13	1.80	0.19	0.9976
Error	13	9.68		



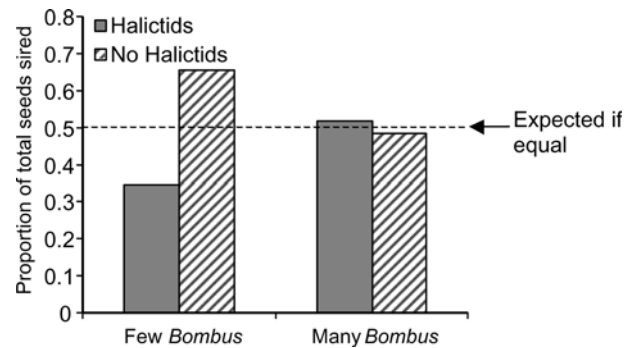
**Fig. 3** The number of halictid visits to *C. americana* flowers with pollen versus flowers without pollen in experimental arrays in the Mountain population. Arrays were categorized by the pollen colors of the flowers with pollen. Asterisks indicate significant tests for the effect of pollen presence for each array color (\*\* $P < 0.01$ )

Do ugly pollinators affect male reproductive success in *C. americana*, and does the presence of efficient pollinators alter this effect?

The effects of halictid visitation rate on siring success depended on the *Bombus* visitation treatment ( $\chi^2 = 9.46$ ,  $P = 0.0021$ ). Halictid visitation decreased relative siring success in the low *Bombus* visitation treatment ( $\chi^2 = 8.05$ ,  $P = 0.0045$ ); the number of halictid visits did not significantly affect siring success in the high *Bombus* visitation treatment ( $\chi^2 = 1.41$ ,  $P = 0.23$ ).

Similarly, the effect of the halictid treatment (present vs. absent) on siring success depended on the number of *Bombus* visitors present (halictid  $\times$  *Bombus*  $G = 6.94$ ,  $df = 1$ ,  $P < 0.008$ ). When *Bombus* visits were infrequent, plants receiving halictid visitors sired 47% fewer seeds than plants where halictid visitation was prevented ( $G = 12.28$ ,  $df = 9$ ,  $P < 0.005$ ; Fig. 4). In contrast, there was no significant difference in siring success between plants receiving halictid visits versus those not receiving halictid visits when *Bombus* visits were common ( $G = 0.205$ ,  $df = 9$ ,  $P >> 0.05$ ; Fig 4).

The different effects of halictids on siring success in the two *Bombus* visitation treatments were not likely due to differences in halictid abundance. Arrays in the two *Bombus* visitation treatments did not differ in halictid abundance (mean number of halictids  $\pm$  SE, low *Bombus*  $17.36 \pm 2.45$ , high *Bombus*  $24.09 \pm 5.04$ ;  $F_{1,20} = 1.44$ ,  $P = 0.244$ ). There also appeared to be no difference in the



**Fig. 4** Proportion of seeds sired by plants receiving halictid visits vs. plants not receiving halictid visits when efficient pollinators were rare (*Bombus*=6) and common (*Bombus*=30). The line  $y = 0.5$  denotes the null hypothesis of equal siring success of the two sires

amount of pollen limitation between the *Bombus* visitation treatments. Low vs. high *Bombus* visitation treatments did not differ in the number of flowers per array that set fruit (mean  $\pm$  SE low *Bombus* treatment  $7.54 \pm 0.83$ , high *Bombus* treatment  $9.00 \pm 0.83$ ;  $F_{1,20} = 1.54$ ,  $P = 0.23$ ) or the number of seeds per fruit (mean  $\pm$  SE low *Bombus* treatment  $15.07 \pm 1.26$ , high *Bombus* treatment  $12.14 \pm 1.12$ ;  $F_{1,19} = 0.36$ ,  $P = 0.55$ ). Additionally, fruits sired by the different halictid treatments did not differ in the number of seeds (mean  $\pm$  SE halictids absent  $10.93 \pm 1.48$ , halictids present  $13.51 \pm 1.86$ ;  $F_{1,71} = 0.97$ ,  $P = 0.33$ ); however, seed production was low in all treatments.

## Discussion

In *C. americana*, halictid bees have greater visitation rates to male-phase flowers with pollen than those without pollen suggesting that they use pollen presence as a floral cue. The use of pollen or other male reproductive floral organs as floral attractants is consistent with results documented in other systems (Solomon 1987; Ashman 2000), including other *Campanula* spp. (Cresswell and Robertson 1994). By using sex-specific structures as floral cues, pollinators may preferentially visit one sex morph more than others. Such selectivity among different sexed flowers has been documented in several monoecious (Bawa 1977), dioecious (Ågren et al. 1986; Bierzychudek 1987), gynodioecious (Ashman and Stanton 1991; Eckhart 1991; Delph and Lively 1992; Eckhart 1992; Jordano 1993; Ashman 2000), and protandrous (Bell et al. 1984; Inoue et al. 1995; Johnson et al. 1995) species. This gender-based preference may represent a cost of spatially or temporally separated male and female reproductive functions (Bierzychudek 1987; Charlesworth 1993; Ashman 2000). Such a cost appears to be present in the protandrous *C. americana* as halictids selectively visit flowers with pollen and decrease the male fitness of plants that they visit when efficient pollinator visits are rare. To our knowledge, this is the first manipulative experiment to document a cost of protandry due to gender-based preferences of low-efficiency pollinators.

## The role of low-efficiency pollinators in floral trait evolution

Pollinators vary widely in their vector pollinating efficiency (sensu Inouye et al. 1994). The halictid visitors of *C. americana* are extremely low-efficiency pollinators and have previously been dubbed “ugly” pollinators because of their tendency to visit and consume pollen from male-phase flowers while avoiding female-phase flowers (Johnson et al. 1995). While there is much evidence that pollinator species vary in their efficiency (Spears 1983; Schemske and Horvitz 1984; Fishbein and Venable 1996), the evolutionary effects of such variation in efficiency are poorly understood.

With low-efficiency pollinators, increasing floral attractiveness may not always benefit fitness. If different pollinators use the same floral cues, then traits that serve to increase attractiveness to beneficial pollinators might be under opposing selection from the negative effects of low-efficiency pollinators (Mazer and Meade 2000). Alternatively, if different species of pollinators use different floral cues (Stanton et al. 1991; Eckhart 1992), selection by ugly pollinators may be an independent force driving floral trait evolution. In our study system, only halictids demonstrated any response to pollen presence, and these halictid visitors were less likely to discriminate against flowers without pollen when the flowers with pollen had purple-colored pollen. If this result translates into more visits to female-phase flowers on plants with purple-colored pollen, then the negative fitness impact of halictids may be overcome and selection for purple-colored pollen may dominate in areas with abundant halictids.

### Variation in the fitness effects of halictids

Halictids decreased the fitness of plants they visited only when high-efficiency pollinators were scarce. There was no fitness effect of halictid visitation when *Bombus* visits were frequent. Since halictids were equally abundant under both low and high *Bombus* conditions, our result suggests that the fitness effects of halictids can be minimized by increased visits from high-efficiency pollinators. *C. americana*'s pollen-collecting hairs prevent halictids from consuming all of a flower's pollen during one visit. Therefore, for a few hours post anthesis, small amounts of pollen likely remain for *Bombus* visitors. If a plant receives many *Bombus* visits, even the small amount of pollen available may be cumulatively large enough across all flowers on the plant to ensure enhanced siring success. However, if a plant receives only a few *Bombus* visits, perhaps the amount of available pollen is too small to ensure equivalent siring success to those plants whose available pollen has not been reduced by halictid consumers. Thus, the relationship between halictids and *C. americana* may range from negative to neutral depending on the relative abundance of other pollinators in the community. In areas where *Bombus* are rare and halictids dominate (e.g., the Mountain population), one

may expect that halictids are a fitness detriment to *C. americana*. In contrast in areas where *Bombus* visitors are relatively more abundant (e.g., the River population), then halictids may have minimal fitness effects on *C. americana*.

Temporal and spatial variation in the frequency of halictid and *Bombus* visitors in these different environments may contribute to the geographical variation in pollen color observed among *C. americana* populations on Salt Pond Mountain. We have documented fitness consequences of halictid visitation when efficient pollinators are rare and differential effects of pollen color on halictid selectivity. Taken together, our results suggest that plants with purple-colored pollen may partially ameliorate the negative fitness consequences of halictid visitation by decreasing halictid selectivity for flowers with pollen and increasing the number of visits to flowers without pollen, and potentially to female-phase flowers. This correlates well with the observed distribution of pollen colors and the relative abundances of low- and high-efficiency pollinators in the community. At the River population, tan-colored pollen is the dominant morph, but the abundance of *Bombus* visitors likely minimizes the negative fitness effects of halictids on *C. americana* fitness. In contrast, the rarity of *Bombus* visitors in the Mountain population may allow for strong negative effects of halictid visitors on *C. americana* siring success. However, purple-colored pollen is the predominant morph in this population, and the decreased selectivity of halictids in arrays with purple-colored pollen may reduce the negative fitness effects of halictids.

In conclusion, we have demonstrated that low-efficiency pollinators can actually decrease male fitness in plants. Therefore, caution is advised in assuming that pollinator visitation rates translate directly to increased plant fitness. We have also demonstrated that floral traits influence the visitation patterns of low-efficiency pollinators. This combination of results supports the idea that ugly pollinators can directly affect floral trait evolution via their negative effects on plant fitness.

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