

# ARE FLOWER-VISITING ANTS MUTUALISTS OR ANTAGONISTS? A STUDY IN A GYNODIOECIOUS WILD STRAWBERRY<sup>1</sup>

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Ants are common flower visitors, but their effects on plant reproductive fitness have not often been assessed. Flower-visiting ants were studied to determine whether they are antagonists or mutualists and whether they could influence floral or breeding system evolution in gynodioecious wild strawberry (*Fragaria virginiana*). Ant and flying pollinator (bees/flies) access to plants was manipulated, and visitation, fruit, and seed set were assessed. Ants visited flowers of hermaphrodites more often than those of females when bees and flies were excluded, but visited the sex morphs equally when they were present. Insect class did not influence fruit or seed set of hermaphrodites. In contrast, ants had both positive and negative effects on seed set in females. Females visited only by ants had 90% of the seed set of those visited only by bees/flies, and their seed set increased with ant visitation. The spatial pattern of seed set, however, suggests that ants may also damage pistils. Lastly, in contrast to bees and flies, ants failed to increase visitation with floral display size, suggesting that ant presence at flowers could reduce selection on this attractive trait. Findings suggest that when in high abundance, flower-visiting ants could affect breeding system and floral evolution in this gynodioecious plant.

**Key words:** ant–plant interaction; ant pollination; floral evolution; *Fragaria virginiana*; gynodioecy; pollination; Rosaceae; sexual dimorphism.

Ants are common flower visitors, and their interactions with plants can take a variety of forms. In some plant species, ants can act as mutualists. Recent work has shown that ants can be effective pollinators especially in plant species with a low, dense flowering stature (reviewed in Beattie, 1985; Gomez and Zamora, 1992; Gomez et al., 1996; Gomez, 2000) and in those growing in Mediterranean and alpine habitats where ant visitation rates can be higher than other floral visitors (Gomez et al., 1996). In other situations, ants can act as antagonists. They may negatively affect plant reproductive success by removing nectar without pollinating (acting as nectar thieves), by disrupting the visitation of effective pollinators and thus reducing pollination (Wyatt, 1980; Fritz and Morse, 1981), or by damaging reproductive structures such as pistils, ovaries (Puterbaugh, 1998; Galen, 1999), or pollen (e.g., Beattie et al., 1985; Wagner, 2000; Galen and Butchart, 2003). Given that both mutualists and antagonists affect plant reproductive success, but in opposite ways, it is important to characterize the interaction between plants and flower-visiting ants.

Moreover, if the type of ant–plant interaction varies with plant reproductive phenotype, then ants could affect floral and/or breeding system evolution (e.g., Galen, 1982; Puterbaugh, 1998; Galen and Cuba, 2001). In particular, if ants act as pollinators yet do not selectively visit plants or if their visitation preferences (Table 1) oppose those of flying pollinators (Ashman, 2000), then ant presence in flowers could obscure or nullify the selection on floral features exerted by flying pol-

linators. Alternatively, if ants are antagonists and they have similar visitation preferences to those of effective pollinators, then ant-mediated negative selection may oppose pollinator-mediated positive selection on attractive traits (e.g., Galen, 1982; Galen and Cuba, 2001). In addition, recent work in two gynodioecious species demonstrated that sex-biased interactions with ants can influence female to hermaphrodite fertility ratios, and thus the maintenance of the gynodioecious breeding system (Puterbaugh, 1998). Sex-differential interactions may come about because sex morphs differ in their reliance on legitimate pollinator visitation to deliver pollen (females are obligately cross-pollinated, whereas hermaphrodites may be able to self-pollinate), or because the detrimental effects of ants are sex-dependent. Thus, because ants have been reported as flower visitors in several gender dimorphic species (Table 1), they could have important effects on both the evolution of sexual system and of sexual dimorphism in secondary sexual traits, but we currently have little data to address this issue.

We conducted ant- and flying-pollinator exclusions and recorded flower visitation, fruit, and seed set in the wild strawberry *Fragaria virginiana* Duch. (Rosaceae), a creeping perennial herb with a gynodioecious breeding system. We sought to answer the following questions: (1) Are ants antagonists? Specifically, do they reduce visitation by known, effective flying pollinators, and/or does their visitation reduce fruit or seed set? (2) Are ants mutualists? Specifically, are they effective as pollinators? (3) Are the effects of ants similar for female and hermaphrodite plants? And last, (4) do ant and flying pollinators respond similarly to floral display?

## METHODS

**Study system**—*Fragaria virginiana*, the Virginian wild strawberry, is a gynodioecious perennial herb that is native to eastern North America (Staudt, 1989). It grows in disturbed areas, fields, and wood edges, and flowers from late April until mid-June. Both sex morphs produce white, bowl-shaped flowers and fleshy receptacles with numerous uniovulate carpels (Staudt, 1989),

<sup>1</sup> Manuscript received 22 September 2004; revision accepted 4 February 2005.

The authors thank Sarah Berman, Alexis Carulli, Denise Cole, Carrie Evnovski, Cassie Majetic, Janette Steets, Sarah Papperman, and two anonymous reviewers for comments on the manuscript and/or help in the field, and John Rawlins and Vanessa Verdecia for ant identification. This research was supported by the National Science Foundation (DEB 9903802 and 0108099 and REU supplement to TLA). This is contribution number 163 to the Pymatuning Laboratory of Ecology.

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TABLE 1. Summary of studies reporting flower-visiting ants in gender dimorphic species (GD: gynodioecious, D: dioecious). We report whether the study found ants to have a positive effect (+) on plants by acting as pollinators or a negative effect (–) by acting as herbivores or nectar thieves, or whether their effect on plants is unknown (?). If ants had a sex-differential effect, the response variable and direction of effect is noted.

Species	Breeding system	Ant effect	Sex bias	Reference
<i>Borderea pyrenaica</i>	D	+	Visitation: F < M	Garcia et al., 1995
<i>Honkenya peploides</i> var. Major	D	?	?	Tsukui and Sugawara, 1992
<i>Myristica insipida</i>	D	?	Visitation: F > M	Armstrong and Irvine, 1989
<i>Nepenthes gracilis</i>	D	?	?	Kato, 1993
<i>Phyllanthus pinnatus</i>	D	?	?	Reddi and Reddi, 1985
<i>Polyscias pancheri</i>	D	?	Visitation: F > M	Schlessman et al., 1990
<i>Eriochromis arietodes</i>	GD	–	Seed set: F < H	Puterbaugh, 1998
<i>Fragaria virginiana</i>	GD	+/-	Visitation: F > H Visitation: F < H or F = H Seed set: F > H	Ashman, 2000 This study
<i>Orchradenus baccatus</i>	GD	?	Visitation: F < H	Wolfe and Shmida, 1995
<i>Paronychia pulvinata</i>	GD	+	Seed set: F > H	Puterbaugh, 1998

hereafter “fruit” with “seeds.” Anthers of hermaphrodites are yellow and are borne on long filaments, whereas those of females are vestigial, white, and devoid of pollen. Whereas females require cross-pollination to set seed, hermaphrodites self-pollinate about half the time ( $s = 0.62 \pm 0.31$ ) and can do so both autogamously and geitonogamously (Ashman, unpublished data). Flowers of hermaphrodites produce more nectar and have petals that are ~50% larger than those of females (Ashman, 2000). Flower visitors include small native bees (including several species of Apidae, Halictidae, Andrenidae, and Megachilidae) flies (including species of Bombyliidae and Syrphidae), and ants (Ashman, 2000). Ants can be major flower visitors in some populations and at some times, i.e., early in the flowering season when they can constitute >80% of flower visitors (Ashman, 2000). In wild populations, bees and flies show a consistent preference for flowers of hermaphrodites, while ants appear to prefer those of females (Ashman, 2000).

**Experimental setup**—This study was conducted at the Pymatuning Laboratory of Ecology (PLE) in Crawford County, Pennsylvania, USA. We located several ant mounds in an open field at PLE (41°34'07" N and 80°27'30" W) and constructed five experimental plots, each within 50 cm of an ant mound. Plots 1–4 were near wood edges, whereas plot 5 was farther out in the open (~30 m from the wood edge). Each plot was enclosed under deer netting and consisted of 28 plants grown in 370-cc pots under common laboratory procedures (see Ashman and Diefenderfer, 2001). Plants within each plot were then manipulated to obtain the following three treatment categories: (1) 10 control plants were left accessible to bees, flies, and ants (hereafter “All” treatment). (2) 10 plants had Tanglefoot (Tanglefoot Co., Grand Rapids, Michigan, USA) applied to the interior and exterior perimeter of their pots. This treatment excluded ants, but left plants accessible to known effective and winged pollinators, bees and flies (hereafter “Bees/Flies” treatment). (3) Eight plants were placed under netted “food umbrellas” (Robinson Knife Company, Springville, New York, USA). These were accessible to ants, but excluded winged pollinators (hereafter “Ants” treatment). This provided us with a total of 140 experimental plants, with each treatment category within each plot composed of half female and half hermaphrodite individuals. Treatments were assigned randomly to plants prior to flowering; and each pot was submerged 7.5 cm in the ground, separated from the nearest neighbor by 4 cm; and sex morphs were alternated so that neighboring plants were of opposite sex. During the experiment, we maintained conditions such that ants could not gain access to Tanglefoot-treated plants by trimming encroaching grass and runners near these individuals. If ants were found on these plants, then their presence was recorded and they were removed.

**Flower visitors**—During 17 observation periods of 10 min each over 11 d in May 2004 at each garden, we recorded the number of open flowers per plant and the number of ant, bee, and fly visits to specific flowering plants. We recorded 339 ant and 361 flying insect (297 bees, 64 flies) visits during

14.2 h of observation. We collected two ants from flowers in each plot. These were identified, and voucher specimens were filed at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA).

**Fruit and seed set**—When flowering was complete, we moved plants to a portable greenhouse to allow fruits to mature. For each plant, we recorded the number of flowers and fruits, and removed and stored fruits in 70% ethanol. In the lab, we randomly selected four fruits from each experimental plant and enumerated fertilized seeds and deflated seeds with the aid of a dissecting scope. We estimated fruit set as the ratio of fruits to total flowers and seed set as the ratio of fertilized seeds to total potential seeds (fertilized seeds plus deflated seeds). The average of the four seed set values per plant was used in analyses.

**Statistical analysis**—We analyzed visitation rate with repeated measures analyses of variance, with sex and treatment as fixed effects, and observation period (time) as a random and repeated effect. Plot was included as a fixed blocking factor. After an arcsine square-root transformation of data for fruit and seed set, we performed ANOVA with sex and treatment as fixed effects and plot as a fixed blocking factor. Because the effect of plot was never significant in fruit and seed set analyses, it was removed from the remainder of these analyses. Comparisons between the All and Bees/Flies treatment groups allow us to determine if ant visitation has detrimental effects on fruit or seed set, whereas comparisons between Bees/Flies and Ants treatment groups allow us to determine if ants are effective pollinators. We used regression analyses to determine if ant and flying insect visitation (average visits  $\cdot$  flower<sup>-1</sup>  $\cdot$  10 min<sup>-1</sup>) responded similarly to increases in floral display size (average open flowers/plant) for the sex morphs separately. For the regression on ant visits, we used data recorded on plants where ants had access (Ants and All treatment groups), and for flying insect visitation, we used data on plants where bees and flies had access (Bees/Flies and All treatment groups). In each case, no significant differences were seen between the two pooled treatment groups (all  $P > 0.20$ ). All analyses were conducted with the SAS statistical package (SAS, 1996).

## RESULTS

**Ant visitors**—Three species of ants were collected from *Fragaria virginiana* flowers: *Prenolepis imparis* (Formicinae) (plots 1 and 2), *Formica subsericea* (Formicinae) (plots 3 and 5), and *Tapinoma sessile* (Dolichoderinae) (plot 4). Ants of each type, however, were seen visiting flowers and foraging for nectar at every plot.

**Flower visitation**—When considering All and Ants treatments only, ant visitation was not significantly affected by

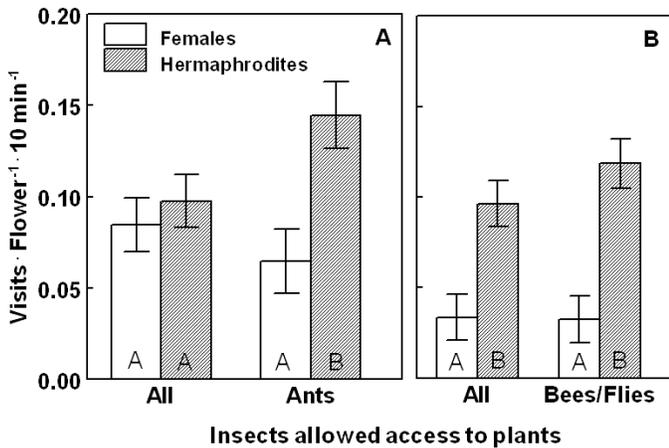


Fig. 1. Mean (±SE) insect visitation rate to female and hermaphrodite *Fragaria virginiana* flowers under different flower visitor treatments. (A) Ant visitation. (B) Bee and fly visitation. Within treatments, sex morphs not sharing the same letter are significantly different.

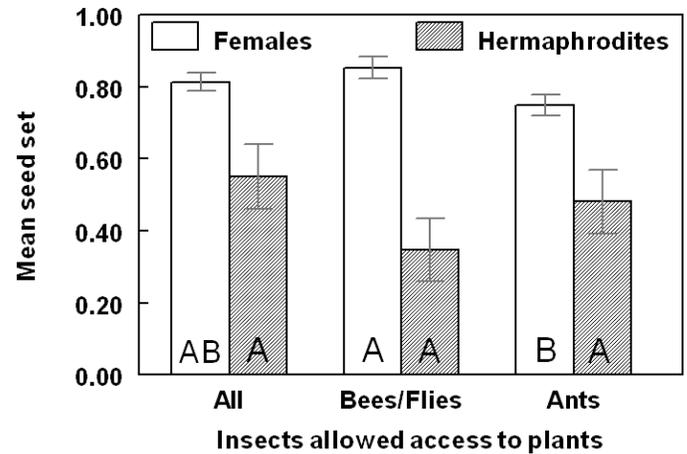


Fig. 2. Mean (±SE) seed set in female and hermaphrodite *Fragaria virginiana* flowers under different flower visitor treatments. Within sex morphs, treatments not sharing letters are significantly different as determined by Tukey's test.

treatment ( $F_{2,1137} = 0.82$ ;  $P > 0.35$ ), but was significantly affected by sex ( $F_{1,82} = 7.45$ ;  $P < 0.01$ ) and by the interaction between sex and treatment ( $F_{2,1137} = 3.80$ ;  $P = 0.051$ ). Ants had a significantly stronger preference for hermaphrodites over females when bees and flies were excluded ( $F_{1,461} = 7.34$ ;  $P < 0.01$ ) than when they were allowed ( $F_{1,676} = 0.46$ ;  $P > 0.50$ ). (Ants visited hermaphrodites 1.16 times more often than females when only ants had access to flowers, but only 0.15 times more often when bees and flies also had access to flowers; Fig. 1A.) There also was significant temporal (time effect:  $F_{16,1137} = 2.39$ ;  $P < 0.002$ ) and spatial (plot effect:  $F_{4,130} = 15.30$ ;  $P < 0.0001$ ) variation in ant visitation. In particular, plot 5 had significantly higher ant visitation than the other four plots (0.244 visits vs. a range of 0.038 to 0.102 visits · flower<sup>-1</sup> · 10 min<sup>-1</sup>).

As in past work, bees and flies showed strong preferences for hermaphrodite flowers over female flowers (mean ± SE, female vs. hermaphrodite: 0.033 ± 0.009 vs. 0.108 ± 0.009 visits · flower<sup>-1</sup> · 10 min<sup>-1</sup>;  $F_{1,92} = 32.73$ ;  $P < 0.0001$ ). Tanglefoot was 90% effective at removing ants (ant visitation in Bees/Flies vs. All: 0.011 vs. 0.91 visits · flower<sup>-1</sup> · 10 min<sup>-1</sup>), but ant removal did not appear to have a major impact on bee and fly visitation rate to the sex morphs (treatment:  $F_{1,1311} = 0.66$ ;  $P > 0.40$ ). There was, however, a 22% increase in visitation to hermaphrodites when ants were excluded, although it was not significant (sex × treatment:  $F_{1,1311} = 0.80$ ;  $P = 0.37$ ; Fig. 1B). Again, there was significant temporal (time:  $F_{16,1311} = 19.73$ ;  $P < 0.0001$ ; time × sex:  $F_{16,1311} = 5.24$ ;  $P < 0.0001$ ) and spatial (plot effect:  $F_{4,92} = 5.52$ ;  $P < 0.001$ ) variation in visitation. In particular, plot 5 had significantly lower bee and fly visitation than the other four plots (0.014 visits vs. a range of 0.068 to 0.098 visits · flower<sup>-1</sup> · 10 min<sup>-1</sup>).

Ants and flying pollinators responded differently to floral display. Regression analyses revealed that bees and flies significantly increased visitation with increasing numbers of open flowers on both female and hermaphrodite plants ( $\beta' = 0.400$ , 0.523;  $R^2 = 0.15$ , 0.27;  $N = 50$ , 50; both  $P < 0.005$ , respectively), whereas ants did not respond significantly to floral display size in either sex morph ( $\beta' = 0.159$ , 0.021;  $R^2 = 0.03$ , 0.001;  $N = 40$ , 40; both  $P > 0.30$ ).

**Fruit and seed set**—While the sex morphs differed in fruit set (mean ± SE, female vs. hermaphrodite: 0.93 ± 0.008 vs. 0.10 ± 0.024;  $F_{1,133} = 764.83$ ;  $P < 0.0001$ ), treatment had no main ( $F_{2,133} = 1.59$ ;  $P > 0.20$ ) or interactive ( $F_{2,133} = 0.49$ ;  $P > 0.60$ ) effect on fruit set. For seed set, there was a significant effect of sex ( $F_{2,95} = 57.58$ ;  $P < 0.0001$ ), no main effect of treatment ( $F_{2,95} = 1.54$ ;  $P > 0.20$ ), but a significant interaction between treatment and sex ( $F_{2,95} = 3.88$ ;  $P = 0.024$ ). For females, seed set was highest in the Bees/Flies treatment group, lowest in the Ants group, and in the middle in the All group ( $F_{2,67} = 4.29$ ;  $P = 0.018$ ; Fig. 2). For hermaphrodites, treatment had no effect on seed set ( $F_{2,23} = 1.31$ ;  $P > 0.20$ ; Fig. 2). Flying insects and ants are effective pollinators in both sex morphs at the level of fruit set, and at the level of seed set for hermaphrodites but not for females. For females, bees/flies may be more effective than ants, or ant visitation may have slight detrimental effects on seed set.

To explore these possibilities further, we analyzed for a correlation between visitation and seed set in females across plots. Seed set in the Ants treatment increased significantly with ant visitation ( $r_s = 0.90$ ;  $P = 0.037$ ;  $N = 5$ ), suggesting that visitation was limiting seed set when ants were the only insect with access to flowers. In contrast, seed set in the Bees/Flies treatment increased, but not significantly, with increasing bee and fly visitation ( $r_s = 0.60$ ;  $P = 0.28$ ;  $N = 5$ ), suggesting that their visits were not limiting under these experimental conditions. In addition, we scored the pattern of seed set on fruits of females visited only by ants and those visited only by bees and flies. Deflated ovules were more common at the base (near the nectaries) of the fruit (swollen receptacle) than anywhere else on the fruits from the Ants compared to the Bees/Flies treatment group ( $\chi^2 = 5.03$ ;  $P = 0.021$ ;  $df = 1$ ;  $N = 88$ ), suggesting that ants may damage pistils near the nectaries when foraging for nectar.

## DISCUSSION

Our work suggests that flower-visiting ants are mutualistic, but may also be antagonistic in *Fragaria virginiana*, and their effects differ between the sex morphs. We discuss our findings and the potential consequences for sexual system and floral evolution next.

**Flower visitation**—The antagonistic interactions between ants and flying pollinators in this system have both direct and indirect components. Specifically, because the removal of bees and flies significantly increased ant visitation rate to hermaphrodites and there was an indication that flying pollinator visitation to hermaphrodites could be enhanced when ants were removed (Fig. 1A, B), our data suggest that ants compete with bees and flies for nectar produced by hermaphrodite flowers. In addition, aggressive interactions between ants and bees were seen for the larger ant (*Formica subsericea*: 4.5 mm), but not for the two smaller species (*Prenolepis imparis* and *Tapinoma sessile*: 2–3 mm) (Ashman and King, personal observation). Few other data on interactions between ants and flying pollinators are available for comparison, but Wyatt (1980) deduced from pollinia removal/receipt data that nectar-thieving ants increased the number but reduced the residence time of butterfly pollinators in *Asclepias curassavica*. The importance of these interactions will depend on the relative effectiveness of ants vs. bees and flies as pollinators.

Competitive interactions between ants and flying pollinators and plasticity in ant visitation patterns may explain the variability in the pattern of ant visitation to the sex morphs. In two wild populations of *F. virginiana*, ants strongly over-visited female flowers while flying pollinators over-visited hermaphrodites (Ashman, 2000). In contrast, in our experiments, ants over-visited hermaphrodites when bees and flies were excluded, and visited the sex morphs equally when they were present. Taken together these data suggest that ants are opportunists that respond to locally available nectar resources, which are modified by the abundance and preferences of other nectar foragers. This may also explain why ants over-visit female plants in several, but not all, dimorphic species (Table 1). This behavioral plasticity combined with the effects of ants on reproductive success could have consequences for mating system, sexual, and gender dimorphism.

**Effects of ants on fruit and seed set**—The effect of flower visitor treatment on seed set was gender morph-specific. Ants had both positive and negative effects on seed set of females (Fig. 2). Ants were effective at pollinating females because their seed set following ant pollination was almost 90% of that via flying-insect pollination and increased with increasing ant visitation among plots. Thus, our work joins that of others in indicating that ants can be as good, or nearly as good, as winged pollinators at pollination (Gomez and Zamora, 1992; Gomez et al., 1996; Puterbaugh, 1998) and that they may have the greatest impact as pollinators when their visitation rates are high. For *Fragaria virginiana* females, however, this positive effect may also come with a negative one because the incidence of deflated ovules around the base of their receptacles (near the nectaries) was elevated in the Ants treatment group, suggesting that ants may damage pistils when foraging for nectar. After finding a similar pattern in *Polemonium viscosum*, Galen and Butchart (2003) concluded that nectar thieves may more often have a negative effect on female than male reproductive success because of the close proximity of ovaries to nectaries.

Our work also joins those on other gender dimorphic species (Table 1) in providing strong evidence that ants can effect cross pollination as seed produced by females is obligately outcrossed. Studies of effective ant pollination in self-compatible hermaphrodite species, on the other hand, could reflect the transfer of a combination of self- and outcrossed pollen.

In fact, Ramsey (1995) used flower manipulations to show that ant pollination in hermaphrodite *Blandfordia* was the result of self-pollination only. In addition, the efficacy of ant pollination of females in gender dimorphic species may depend on the frequency of visits to females relative to pollen-bearing morphs (hermaphrodites). Here, visitation was equivalent (All) or hermaphrodite-biased (Ants), but when visitation is female-biased, the negative effect of ant visitation on seed set may outweigh the positive effects. For instance, in a wild population where ants preferred to visit female flowers, Ashman (2000) found that pollen receipt by females decreased with increasing abundance of ants. This may result from the negative effect ants have on flying pollinator visitation to hermaphrodites and/or because ants that only visit females transport no pollen.

Flower visitor treatment had no differential effect on fruit or seed set in hermaphrodites, possibly because they are capable of autogamous self-pollination (Ashman laboratory, unpublished data). However, ant visitation might influence hermaphrodite selfing rate by altering the ratio of self- vs. outcross pollination either directly or via interactions with flying pollinators. Ants may also affect hermaphrodite outcross siring ability if their visitation reduces pollen viability (Wagner, 2000), flying pollinator residence times (Wyatt, 1980), or flight distances. All of these avenues for ant effects in hermaphrodites warrant additional work, because only one study has considered any of them (Galen and Butchart, 2003).

**Consequences for floral and breeding system evolution**—Because ants have both negative and positive effects on female seed set, their effect on floral or breeding system evolution will depend on the availability of other pollinators. When flying pollinators are rare, the benefit of ant visitation will outweigh its cost, but when flying pollinators are abundant, the cost of ant visitation may be more substantial. Although this study did not explore a huge panel of potential traits that attract ants to plants, it did show that their preference for hermaphrodites over females was context dependent and that they do not respond to open flower display size. In contrast, flying pollinators consistently prefer hermaphrodites and large floral displays (Ashman et al., 2000; Ashman and Diefenderfer, 2001; Case and Ashman, unpublished manuscript). Thus, if pollen receipt is limiting seed fitness, then the presence of ants at flowers could reduce net selection on floral display size. A larger panel of traits needs to be assessed to determine other traits that may be subject to ant-mediated selection.

As antagonists, ants could affect breeding system evolution, either the maintenance of gynodioecy or the evolution of dioecy, by influencing the relative fertility of the sex morphs (female to hermaphrodite [F : H] seed fertility ratio), the selfing rate of hermaphrodites, or the pollen fitness gain curve (Ashman, 2002). Here we only explored the potential sex-biased effect on seed production. Our results, combined with those of Ashman (2000), suggest that ants may reduce F : H seed fertility ratio when ant visitation is high relative to flying pollinators. Puterbaugh (1998) also found that ants reduced the F : H seed fertility ratio, suggesting that the presence of ants at flowers in gynodioecious species should not be ignored. Additional studies are needed to provide rigorous tests of all the ways that ants may influence breeding system parameters.

**Conclusions**—Our work joins that of others in indicating that ants can be as good as bees and flies as pollinators (Go-

mez and Zamora, 1992; Gomez et al., 1996; Puterbaugh, 1998; Gomez, 2000), and adds generality to these findings by (1) showing that females can be ant-pollinated, thereby demonstrating that ants can cross-pollinate, and (2) extending the types of habitats in which ant pollination occurs beyond the alpine and arid lands to meadows and temperate deciduous forests. Moreover, this work suggests that flower-visiting ants can have both positive and negative effects on seed set and thus could obscure or facilitate flying pollinator-mediated selection, depending on ant abundance. And finally, it suggests that ants and flying pollinators compete for nectar, so ant presence could alter other aspects of plant reproductive success, such as selfing rate and male outcross siring success.

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