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# THE CONSEQUENCES OF FLORAL HERBIVORY FOR POLLINATOR SERVICE TO *ISOMERIS ARBOREA*

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*Abstract.* Flower-feeding insects may reduce the reproductive success of their host plant in subtle ways that go beyond a direct reduction in gametes. Pollinators may respond to floral damage by visiting damaged plants at lower rates. Fewer visitations to the plant may result in fewer flowers that receive pollinator service and as a consequence lead to lower male and/or female reproductive success. In a two-year study, we examined the direct effect of flower predation by *Meligethes rufimanus* on the floral display of *Isomeris arborea*, and the indirect effect of herbivory on pollinator behavior. Plants exposed to herbivore attack produced fewer functional inflorescences than plants protected from herbivory. Undamaged flowers produced three times as much nectar per flower as damaged flowers. Likewise, protected plants had over twice as many anthers per flower as exposed plants. Pollinators responded by visiting damaged flowers less, and exposed plants had lower flower visitation rates than protected plants. Pollinators also visited patches of protected plants more frequently than exposed patches. These results show that floral herbivory reduces pollinator service and thus may reduce reproductive success indirectly, as well as through the direct consumption of viable gametes.

*Key words: floral damage; floral display; indirect effect of herbivory;* Isomeris arborea; Meligethes rufimanus; *nectar production; plant–insect interactions; pollination; pollinator visitation rates.*

## INTRODUCTION

Herbivores that feed upon floral structures reduce the reproductive success of many plant species (Breedlove and Ehrlich 1968, Inouye 1982, Zammit and Hood 1986, Schemske and Horvitz 1988, Evans et al. 1989, Wallace and O'Dowd 1989, Pettersson 1991, English-Loeb and Karban 1992, Muenchow and Delesalle 1992, Cunningham 1995). It is reasonable to believe that these reductions are primarily due to the direct loss of gametes. Floral herbivory, however, may hinder plant reproduction indirectly by reducing pollinator service. When herbivores attack flowers, their damage can (1) degrade the advertising properties of each flower, (2) reduce the number of flowers per display, and (3) lower pollinator rewards. Pollinators are known to respond to variation in floral morphology: Studies utilizing either natural variation in flower size (Galen and Newport 1988, Stanton and Preston 1988, Galen 1989, 1996, Young and Stanton 1990, Campbell et al. 1991, Mitchell 1992) or experimental manipulation of petal length (Johnson et al. 1995) have shown that pollinators prefer larger flowers. Intraspecific variation in color (Waser and Price 1981) and scent (Galen 1985) also influences visitation. Pollinators not only respond to attributes of the flowers themselves, but also to the number of flowers, with larger inflorescences usually being the more

attractive (although in many of these cases the proportion of flowers visited actually declines as flower number increases [reviewed in Snow et al. 1996]). Flowers rich in nectar (Zimmerman 1983, 1988, Galen and Plowright 1985, Thomson 1988, Campbell et al. 1991, Real and Rathcke 1991, Mitchell 1993, 1994, Hodges 1995) and other pollen rewards (Harder 1990, Cresswell and Robertson 1994) also can receive more visits than flowers with lower levels. Given this sensitivity in pollinators to floral state, external agents that alter display or reward can alter the plant's chance of being serviced (Strauss 1997). Herbivores can be such agents (Karban and Strauss 1993, Strauss et al. 1996, Lehtilä and Strauss 1997).

We have examined the effects of flower predation on pollinator service and reproductive success in *Isomeris arborea* (Capparaceae), a shrub whose flowers are attacked by a pollen beetle, *Meligethes rufimanus* (Coleoptera: Nitidulidae). This beetle alters floral advertisement: Petals and anthers wilt and the corolla does not completely open. In this paper, we quantify damage to display and rewards, determine if damage reduces service, and ask at what scale (e.g., flower, plant, or neighborhood) pollinators respond to damage. Reduced pollinator service can in turn lead to reduced pollen export and receipt, which reduces reproductive success through male and female function, respectively. A companion paper (Krupnick and Weis 1999) examines the differential consequences of reduced pollinator activity for male and female components of reproductive success.

## METHODS

### Study system

*I. arborea* is a Southern California drought-decid-uous perennial shrub (Munz 1974:330) that can flower from January until November if water is available. The species has a disjunct range, with both Mojave desert populations and coastal populations ranging from Santa Barbara, California, to Northern Baja California, Mex-ico. This self-compatible species is andromonoecious, with hermaphroditic and male flowers produced on the same inflorescence. Bisexual flowers produce six sta-mens and a superior ovary extended on a gynophore; male flowers produce six stamens and a nonfunction-ing, undeveloped pistil. Visitors to the yellow flowers include bumblebees (*Bombus* spp.), nonnative honey-bees (*Apis melifera*), and hummingbirds (*Calypte cos-tae* and *C. anna*). While it is not known which visitor is the most effective pollinator, bumblebees are a likely candidate (Grant and Grant 1967), since they contact all reproductive parts during a visit to a flower (G. A. Krupnick, *personal observation*).

*I. arborea* is host to the pollen beetle, *M. rufimanus*, which feeds on capers and crucifers in northern tem-perate regions. In coastal California, adult beetles feed on pollen from developing and mature *I. arborea* flow-ers between January and June. Females oviposit in de-veloping flower buds. The resulting larvae mature with-in the buds, where they consume developing anthers. Most damaged buds abort (Krupnick 1996), but some flowers succeed in blooming, with a reduced number of functional anthers and possible damage to the ovary wall. At the end of the third instar, the beetle larvae fall to the ground to pupate.

### Study plots and damage manipulation

We evaluated beetle damage and pollinator response in both natural and planted arrays of *I. arborea* within the Ecological Reserve at the University of California, Irvine. The natural population consists of over 200 *I. arborea* shrubs growing on a hill (~75 m in diameter) with other coastal sage scrub species (e.g., *Artemisia californica, Eriogonum fasciculatum,* and *Encelia cal-ifornica*). We manipulated damage levels through in-secticide applications. During 1992, 60 plants within this population received one of three treatments: pro-tection from natural levels of herbivory ("protected"), which results in low levels of damage; exposure to herbivory with a water application ("exposed"), which results in high levels of damage and is a sham-control for spraying; or exposure to herbivory without a water application ("exposed without spray"), which results in high levels of damage. Protected plants were sprayed with a systemic insecticide (Dimethoate CA267, ob-tained from Platte Chemical Company, Fremont, Ne-braska) dissolved in water (29.5 mL/L); exposed plants were sprayed with water only. Both insecticide spray and water were applied at the rate of 40 mL per plant,

once every two weeks, between January and June from 1993 to 1995. *M. rufimanus* is the only herbivore that feeds upon *I. arborea* during this time period (G. A. Krupnick, *personal observation*), and thus it is the only herbivore species being removed by the insecticide treatment. The insecticide treatment has no effect on inflorescence or fruit production of *I. arborea* in a her-bivore-free environment (Krupnick 1996).

The two experimental arrays were planted in January 1993 ~50 m from the natural population. We used ran-domly selected, first-generation offspring from 25 *I. arborea* plants in the natural population. Offspring plants were grown from seed in a greenhouse for one year before transplanting.

"Array 1" was designed to evaluate pollinator re-sponses at three spatial scales: within plant, within patch, and among patches. It contained nine 3 × 3 m plots of 16 plants each. Each plant received either the protected or exposed treatments. In three plots, all plants were protected from herbivory ("protected plots"); in three plots, all plants were exposed to her-bivory ("exposed plots"); and in three plots, half the plants were protected and the other half were exposed ("mixed plots"). Plants in the mixed plots typically received intermediate levels of attack, with protected plants receiving more damage than protected plants in protected plots, and exposed plants receiving less dam-age than exposed plants in exposed plots (Krupnick and Weis 1998).

"Array 2" was a hexagonal grid containing 90 plants spaced 1 m apart, with a diameter of 12 m. Plants were assigned to the exposed and protected treatments at random.

### Effects of beetle attack on floral display

The effect of florivory on flowering display was es-timated on exposed and protected plants by counting the number of developing inflorescences (damaged and undamaged) and the number of flowering inflores-cences on a regular schedule though the flowering sea-son. Developing inflorescences were defined as flower bud clusters without any open flowers. Damaged inflo-rescences showed damage to the corolla of developing buds, whereas undamaged inflorescences showed no sign of damage. Counts were done once every two weeks in 1992 on 30 plants from the natural population, weekly in 1994 on all 144 plants in Array 1, and once every two weeks in 1995 on the 110 surviving Array 1 plants.

We compared the number of undamaged flowering inflorescences on protected and exposed plants using a repeated-measures ANOVA. To control for the effect of plant size, the number of branches (determined at the start of each season) was used as a covariate. The initial number of branches per plant did not differ be-tween herbivory treatments in either year (1994: $F_{1, 143}$ = 1.81, $P > 0.05$; 1995: $F_{1, 143}$ = 1.04, $P > 0.05$). To factor out plot effects in the artificial arrays, we per-

formed two additional repeated-measures ANOVAs examining inflorescence production during the months of *M. rufimanus* activity. We compared plants in fully exposed and fully protected plots with individual plots as a nested variable within herbivore treatment. We also compared exposed and protected plants within the mixed plots. All ANOVAs were conducted using the GLM procedure in PC SAS (SAS Institute 1990).

### Beetle attack and floral rewards

In April 1993, we measured nectar production from 10 damaged and 10 undamaged hermaphroditic flowers from each of six different exposed plants from the natural population. Damaged flowers had chew marks to the corolla and/or missing stamens. Undamaged flowers had no signs of damage to the corolla, pistil, or stamens. We used flowers judged to be a day old based on their position at the bottom of the inflorescence and the appearance of newly dehisced anthers. Nectar was removed with a microcapillary tube from 1-d-old flowers and then covered with a mesh bag. Bags were removed 24 h later and the volume of nectar produced was measured using microcapillary tubes. Production measurements were analyzed by ANOVA, with flower damage as the fixed factor and individual plant as the random factor.

Pollen availability was estimated by counting the number of undamaged dehiscent anthers per flower on all 1–6 d old flowers on six exposed plants and six protected plants in the natural population. This is a conservative measure of pollen production, because anthers on damaged flowers may produce less pollen as a result of the damage to the plant, and some of the pollen produced may be consumed by adult beetles. We used a *t* test to compare the mean number of anthers per flower between the two plant treatments.

### Pollinator observations

To determine the effects of florivory on visitation by pollinators, we observed pollinator activity on individual plants, pairs of plants, and patches of plants in the experimental arrays during April and May in 1994 and 1995. We counted the number of inflorescences and the total number of damaged and undamaged flowers for each plant before each observation period. During each 2-h observation session, observers recorded the identification number of the plant being visited, the species of visitor, the number and condition (damaged or undamaged) of flowers visited, and the number of inflorescences visited. We defined a flower visit as contact between pollinator and flower, and plant visits as at least one flower visit by a visitor before flying to another plant. Each time the same individual pollinator returned to the plant after visiting a new plant, we scored that visit as a new plant visit.

We measured pollinator behavior at three spatial scales: (1) flower level, (2) plant level, and (3) patch level. To measure differences in visitation at the flower

level, 76 plants were observed in total during six 2-h observation sessions in 1994, and 41 plants were observed during four 2-h observation sessions in 1995. These plants were located in either the mixed plots of Array 1 or in Array 2. Each plant under study had both damaged and undamaged flowers. Pollinator visitation rates to damaged and undamaged flowers were calculated as the number of visits per damaged flower per hour and the number of visits per undamaged flower per hour, respectively. Flower visits were defined as above. Pollinator visitation rates were analyzed using paired *t* tests for each year.

To measure responses to damage at the plant level, visitation rates were compared on pairs of adjacent exposed and protected plants. We observed 22 pairs in 1994 and 21 pairs in 1995. For inclusion in this study, exposed plants had to have more than half their flowers damaged (proportion of damaged flowers per plant: mean $\pm$ 1 SE = 0.75 $\pm$ 0.03 [1994], 0.72 $\pm$ 0.03 [1995]). Likewise, protected plants had to have fewer than half their total flowers showing damage (proportion of damaged flowers per plant: mean $\pm$ 1 SE = 0.23 $\pm$ 0.03 [1994], 0.24 $\pm$ 0.03 [1995]). Each pair came from either the mixed plots of Array 1 or from Array 2. Pollinator visitation rates (the number of visits per flower per hour) were analyzed using paired *t* tests for each year.

Finally, for observations at the patch level, we used the protected, exposed, and mixed plots in Array 1. Three plots per treatment were available in 1994, but only two per treatment in 1995. During each 2-h observation period, we concurrently monitored pollinator activity in triplets of plots, with one plot per treatment per period. Every pollinator entering each patch was counted, and all flower visits were tallied for each plot. A "patch approach" was defined as a new pollinator entering a new patch and visiting at least one plant in that patch. We analyzed (1) the pollinator approach rate (number of approaches per hour) per patch, (2) the number of plants visited per approach to a patch, and (3) flower visitation rates to each plant treatment in each patch. For the first level of analysis (patch approach rate), some of the plots in Array 1 were used in both years, and so we first ran a preliminary ANOVA on the approach rate using year as the source of variation. We then averaged the two residuals (one for 1994 and one for 1995) for plots observed during both years to avoid pseudoreplication in our final analysis. Using the averaged residuals for plots with two years of observations and the single residuals for plots with only one observation, we performed an ANOVA on the residuals of approach rate using patch treatment as the source of variation. The second level of analysis examined the number of plants visited at each patch type during a single pollinator patch visit. For this analysis, we used nonparametric Kruskal-Wallis tests due to the nonnormal distribution of data. We compared the mean number of plants visited among the three patch treat-

ments for each year of study. Finally, for the third level of analysis, we examined the frequency of flower visits at each patch type. Using Kruskal-Wallis tests (due to nonnormal distribution of data), we compared the number of visits per flower per hour across different patch treatments for each year of study.

### Morphological manipulations and observations

Floral herbivory may influence floral display, floral morphology, and floral rewards. One way to separate how each of these affects pollinator choice is to simulate herbivore damage by manipulating one of these characters. We examined the effect of floral morphology on pollinator attraction by observing pollinator service to inflorescences in which we simulated insect damage to the anther and petal display. Natural levels of damage by *M. rufimanus* range from partial, in which one or more anthers are destroyed, to extensive, in which the petals are also mutilated (G. A. Krupnick, *personal observation*). On 18 February 1994, 10 protected plants in the natural population were manipulated and observed for pollinator activity. Three inflorescences from each plant were chosen, and undamaged flowers from each inflorescence received one of three treatments: (1) anthers removed, (2) anthers removed and petals clipped, and (3) control. Inflorescences were labeled, and the anthers were removed with scissors (treatments 1 and 2), and ragged margins cut into the petals to simulate beetle damage (treatment 2). During the 1.5-h observation session, we recorded the number of open flowers per inflorescence, the species of each visitor, and the number of flowers visited on each inflorescence. After the observation session, inflorescences were covered with an insect exclusion bag to prevent further damage, and pollinator activity was observed again on the same inflorescences but with new flowers on 25 February 1994. For each date, we calculated the pollinator visitation rate (visits per flower per hour) to each inflorescence for all pollinator species combined. For each observation date, visitation rates were compared among treatments using a randomized-block ANOVA, with plant as the blocking factor. Pairwise comparisons on each of the variables were made using a Tukey-studentized multiple-comparison test.

### RESULTS

#### Floral display

Herbivore damage caused a reduction in the number of functioning, undamaged inflorescences in *I. arborea* plants. In the natural population, plants protected from herbivory produced more active, undamaged inflorescences (with at least one open flower) than plants exposed to herbivory and plants exposed without spray during the 1992 flowering season (Fig. 1a, Table 1). In experimental Array 1, protected plants outproduced exposed plants in both 1994 and 1995 (Fig. 1b and c; Table 1). A 2:1 difference in the number of undamaged
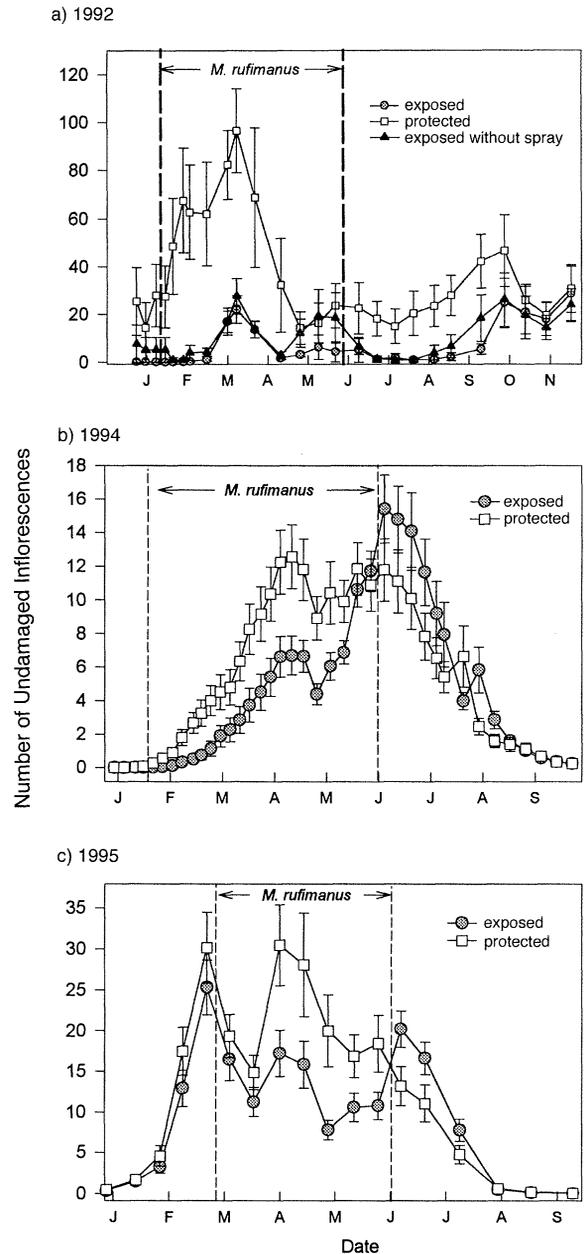


FIG. 1. The production of undamaged flowering inflorescences during the (a) 1992, (b) 1994, and (c) 1995 flowering season for various herbivory treatments of *I. arborea*. Shaded circles show plants exposed to herbivory with water spray; open squares show plants protected from herbivory with insecticide spray; solid triangles show plants exposed to herbivory without water spray. Errors bars indicate ±1 SE. The time between dashed lines indicates feeding activity of *M. rufimanus* on *I. arborea*.

inflorescences was seen during the months of pollen beetle activity. Differences were much less after the beetles had completed development and entered diapause (Fig. 1); data from the experimental array suggest increased late flower production in the exposed plants,

TABLE 1.  Results of repeated-measures ANOVA on inflorescence production in *I. arborea* during 1992, 1994, and 1995.

| Year | Source of variation | df | MS | F |
|------|---------------------|-----|-------|-------|
| 1992 | Between plants | | | |
| | Insecticide treatment | 2 | 184.94 | 17.63*** |
| | Number of branches | 1 | 175.92 | 16.77** |
| | Error | 26 | 10.49 | |
| | Within plants | | | |
| | Date | 25 | 9.68 | 9.83*** |
| | Date × insecticide treatment | 25 | 2.79 | 2.84*** |
| | Date × number of branches | 50 | 1.74 | 1.77* |
| | Error (date) | 650 | | |
| 1994 | Between plants | | | |
| | Insecticide treatment | 1 | 44.03 | 5.28** |
| | Number of branches | 1 | 972.95 | 166.76*** |
| | Error | 141 | 8.33 | |
| | Within plants | | | |
| | Date | 35 | 6.38 | 16.01*** |
| | Date × insecticide treatment | 35 | 4.61 | 11.56*** |
| | Date × number of branches | 35 | 5.01 | 12.56*** |
| | Error (date) | 4935 | 0.40 | |
| 1995 | Between plants | | | |
| | Insecticide treatment | 1 | 17.74 | 4.93* |
| | Number of branches | 11 | 766.13 | 213.02*** |
| | Error | 108 | 3.60 | |
| | Within plants | | | |
| | Date | 13 | 6.52 | 12.17*** |
| | Date × insecticide treatment | 13 | 3.48 | 6.50*** |
| | Date × number of branches | 13 | 5.72 | 10.68*** |
| | Error (date) | 1404 | 0.54 | |

*Note:* Data were $\log(x + 1)$-transformed.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

which in part compensates for earlier damage (Fig. 1). The Array 1 plants were arranged in plots, and these differences between protected and exposed plants could in part reflect variation due to the spatial location of the plot, and so a confirmatory analysis was done to factor out plot effects. During the months of pollen beetle activity in 1994, plants in fully protected plots produced more undamaged inflorescences than plants in fully exposed plots (herbivore treatment: $F_{1,4} = 8.33$, $P < 0.05$; plot [treatment]: $F_{4,89} = 5.45$, $P < 0.0001$; date × treatment: $F_{18, 1602} = 5.88$, $P < 0.0001$). In 1995 our nested analysis revealed only a significant date × treatment interaction (herbivore treatment: $F_{1,89} = 3.78$, $P > 0.05$; plot [treatment]: $F_{4,89} = 5.16$, $P < 0.001$; date × treatment: $F_{1, 356} = 15.37, P < 0.0001$). Exposed and protected plants in mixed plots did not statistically differ in their number of undamaged inflorescences during either year (herbivore treatment: $F_{1,45} = 0.63$, $P > 0.10$ [1994]; $F_{1,45} = 0.32$, $P > 0.10$ [1995]). The similarity of the plants in the mixed plots probably reflects lower beetle densities in these plots. When half the plants are sprayed, enough beetles remain to inflict moderate damage on the exposed plants. These beetles can then move onto protected plants, where they inflict noticeable damage before being killed by the insecticide. Although the number of undamaged inflorescences did not differ between protected and exposed plants in the mixed plots, clear differences in flower number were observed (Krupnick and Weis 1998).

### Floral rewards

Exposure to herbivores greatly reduced floral rewards. Undamaged flowers produced three times more nectar per flower in a 24-h period ($14.95 \pm 1.45$ µL [mean $\pm$ 1 SE]) than herbivore-damaged flowers ($3.28 \pm 0.89$ µL; $F_{1,5} = 41.83, P < 0.01$). Likewise, protected plants had over twice as many pollen-producing anthers per flower ($5.03 \pm 0.24$ anthers) as did exposed plants ($1.96 \pm 0.19$ anthers; $t = 9.97$, df = 10, $P < 0.0001$).

### Pollinator observations

During all 1994 observation periods combined, we observed 301 (94.6%) foraging bouts by bumblebees, 12 (3.8%) by honeybees, and 5 (1.6%) by hummingbirds. In 1995, we observed 52 (85.2%) bouts by bumblebees, 2 (3.3%) by honeybees, and 7 (11.5%) by hummingbirds. Lower visitation rates in 1995 are probably due to the unusually high number of overcast days in that year. Over all, pollinators overvisited the undamaged condition of *I. arborea* in comparison to the damaged condition, and this pattern is evident at all three spatial scales.

At the flower level, undamaged flowers received significantly more visits per hour than did damaged flowers (Fig. 2a). Undamaged flowers received 3.2 times more visits in 1994 (paired *t* test: $t = 5.66$, df = 75, $P < 0.0001$) and 2.7 times more visits in 1995 (paired *t* test: $t = 4.04$, df = 40, $P < 0.0002$).

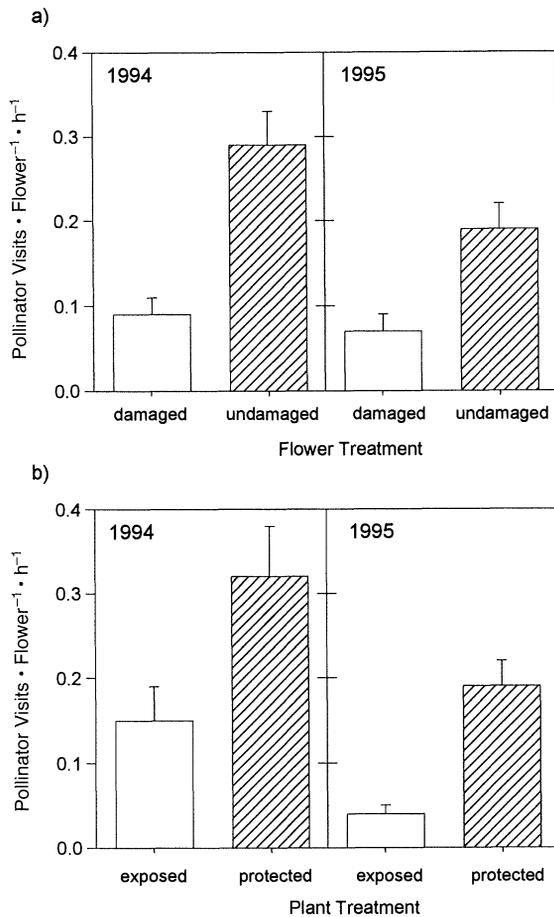Pollinators also visited low-damage plants with

a)



b)



FIG. 2. Pollinator visitation rates to two treatments of *I. arborea* (a) flowers and (b) plants in 1994 and 1995. Bars indicate mean + 1 SE. Flowers were either damaged by herbivory or remained undamaged. Exposed plants were sprayed with water; protected plants were sprayed with insecticide.
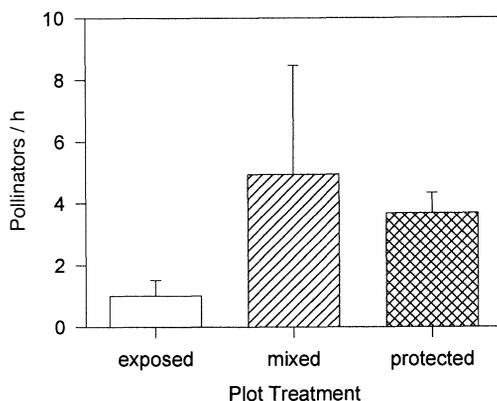


FIG. 3. The mean (+ 1 SE) pollinator approach rate (number of approaches per hour) to to exposed, mixed, and protected plots of *I. arborea*. Exposed plots were sprayed with water; mixed plots had half the plants sprayed with water and the other half sprayed with insecticide; protected plots were sprayed with insecticide.
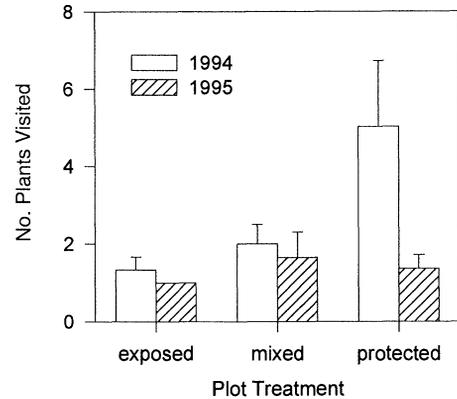


FIG. 4. The mean number (+ 1 SE) of plants visited per pollinator visit at exposed, mixed, and protected plots of *I. arborea*. Plot treatments follow notation in Fig. 3.

greater frequency (Fig. 2b). Protected plants received 2.1 times more flower visitations than exposed plants in 1994 (paired *t* test: $t = 3.55$, df $= 21$, $P < 0.0019$) and 4.8 times more in 1995 (paired *t* test: $t = 4.75$, df $= 20$, $P < 0.0001$).

At the largest spatial scale, patches also differed in visitation rates (Figs. 3–5). Approach rates were greater in patches of lower damage (Fig. 3), although differences were only marginally significant ($F_{2,8} = 3.92$, $P = 0.08$). While visiting a patch, pollinators visited more plants per visit in protected plots than in mixed or exposed plots during 1994 (Fig. 4; Kruskal-Wallis test, $\chi^2 = 6.16$, df $= 2$, $P = 0.0459$), but no difference was found in 1995, when all visitations were down ($\chi^2 = 0.75$, df $= 2$, $P = 0.6873$). In addition, the flower visitation rates differed among the four combinations of plant and plot treatments in both years (Fig. 5; 1994: Kruskal-Wallis test, $\chi^2 = 15.61$, df $= 3$, $P = 0.0014$; 1995: $\chi^2 = 26.98$, df $= 3$, $P = 0.0001$). At this level, pollinators do not seem to "spill over" onto damaged plants where they occur among undamaged ones. This result is consistent with the fine-scale discrimination exhibited by pollinators at the within-plant level.

### Morphological manipulations and observations

Manually damaged inflorescences (anthers removed, or anthers removed and petals clipped) had significantly fewer visits per flower per hour than control inflorescences on 18 February 1994 ($F_{2,14} = 5.57$, $P = 0.0166$; Fig. 6a), but no differences were found among the three treatments on 25 February 1994 ($F_{2,12} = 2.79$, $P = 0.1014$; Fig. 6b). On the earlier date, plants with standing nectar crops were manipulated, whereas on the later date, flowers had been bagged before manipulation, and therefore had full nectar crops. Direct pollinator visual responses to nectar volume could explain the differences in response between dates.

### DISCUSSION

Attack by *M. rufimanus* on *I. arborea* changes floral display and rewards in a number of ways. We previ-
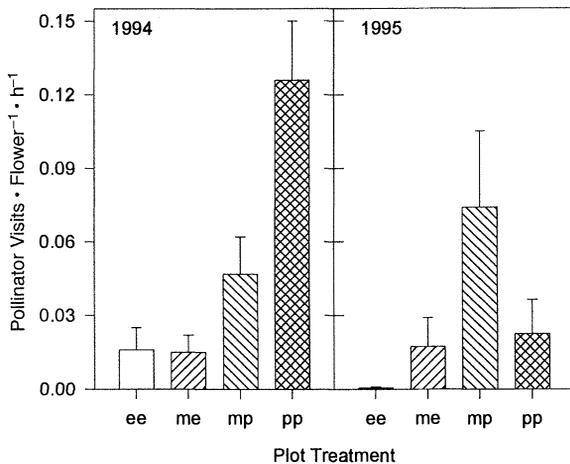
FIG. 5. Pollinator visitation rates to four treatments of *I. arborea* populations in (a) 1994 and (b) 1995. Abbreviations: ee = exposed plants in exposed plots; me = exposed plants in mixed plots; mp = protected plants in mixed plots; and pp = protected plants in protected plots. Bars indicate mean + 1 SE.

ously showed that over the course of the year, beetle attack reduces the number of flowers per inflorescence to a third of that on control plants protected by insecticide (Krupnick and Weis 1998). This flower reduction comes from increased bud and flower abortion. Here we present data showing that, at any one time, an attacked plant has only half as many active, undamaged inflorescences (Figs. 1 and 2). Attacked flowers that survive to anthesis are marked by chewing damage to the petals. Floral rewards are also diminished by attack, with a fourfold decrease in nectar production and at least a threefold decrease in pollen availability. Thus, beetle attack degrades most of the floral elements that attract pollinators. This raises the questions, What is the degree of service reduction caused by damage? and What are the organizational levels at which reductions occur—within the plant, among plants, or among plant neighborhoods?

Highly damaged plants had fewer visits than their healthy counterparts. Part of the reduction is simply because there were fewer open flowers (G. A. Krupnick, *unpublished data*). We have analyzed our results on a per flower basis in order to determine if surviving flowers face a proportionate change in visitation rate.

At the most basic level, an undamaged flower is three times more likely to be visited than a damaged one on the same plant (Fig. 2a). Bees seem to avoid flowers with tattered petals and chewed-off stamens. The decision not to visit appears to be made as the bee hovers over the inflorescence, and so the damaged flower parts may signal the lower rewards inside. We attempted to verify a direct negative response by bees to damage by offering healthy and manually damaged flowers. In the first run of the experiment, when flowers had natural nectar levels, control flowers (undamaged) had at least

a twofold advantage over those with clipped anthers or with both clipped petals and anthers (Fig. 6). This supports the notion that bees respond to the appearance of damage. However, a more ambiguous result was obtained in the second run; flowers with anther and petal damage had the numerically lowest visitation rate, but the difference was not significant. Unlike the first run, inflorescences had been bagged for a week to exclude herbivores and pollinators, so the nectaries of both the control and manipulated flowers were abnormally full. Other investigators have found that high nectar rewards can override normal bee responses to the floral display (Cresswell and Galen 1991). The disparity between the two runs of the manual damage experiment could be explained if foraging intensity is affected by the profitability of the entire inflorescence (Pyke 1981, Best and Bierzychudek 1982). Long-term nectar accumulation could have made the inflorescences unusually valuable and thus prompted bees to stay longer and forage more intensely while paying less regard to flower appearance.
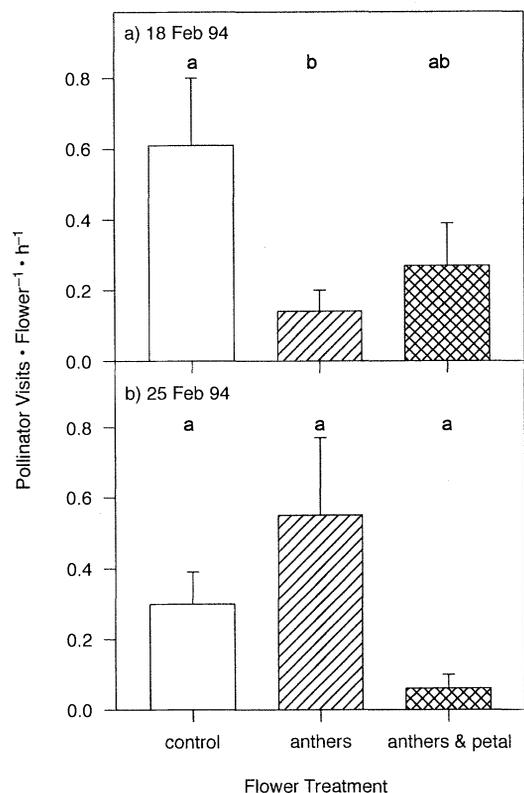
These data show that pollinators respond to damage



FIG. 6. Pollinator visitation rates to *I. arborea* flowers under three hand-manipulated treatments on (a) 18 February 1994 and (b) 25 February 1994. Bars indicate mean + 1 SE. Control = unmanipulated flowers; anthers = anthers removed from flowers; anthers and petal = anthers removed and petals clipped on flowers. Different letters above bars indicate significant differences between the treatments as determined by Tukey-studentized multiple-comparison tests ($P < 0.05$).

at the level of the individual flower, but also open the possibility that they respond to damage at higher organizational levels. According to optimal foraging theory, pollinators should choose high-quality patches to maximize their net rate of energy intake while foraging (Pyke 1984). Several studies show that insect pollinators concentrate their visits in patches of high flower density (Thomson 1981, Gass and Sutherland 1985, but see Schmitt 1983). Thus, the probability of visitation to a flower may depend not only on its own state, but on the profitability of the flowers surrounding it (Armbruster 1988).

For instance, pollinators may avoid entire plants where most of the flowers are damaged. If so, intact flowers on highly damaged plants may receive fewer visits than intact flowers on undamaged plants. This kind of pollinator response would magnify the impact of beetle attack on plant reproductive success, since for every flower actually damaged, several healthy ones could go to waste for lack of pollinator service. The most direct test of this hypothesis is to measure visitation rates of damaged and undamaged flowers on lightly and heavily damaged plants. This was not logistically possible because the shrubs were too large for accurate damage classification of all flowers visited. However, we can compare the observed plant-level visitation rate (damaged and undamaged flowers combined) with the rate that would be predicted if pollinator responses were at the flower level only. We generated this prediction from our observations that (1) within plants, visits to damaged flowers were only 33% as great as undamaged ones (see *Results*), and (2) that in the plant-level comparisons, ~75% of the flowers on exposed plants were damaged, while only 25% were damaged on protected plants (see *Methods*). Assuming that responses are at the flower level only, a healthy flower has an expected visitation rate of $q$, while a damaged one has a visitation rate of $0.33q$. Total visitation rates per flower to protected plants should then be $(0.25 \times 0.33q) + (0.75 \times q)$, where the terms in the first set of parentheses are visits to damaged flowers and those in the second are visits to undamaged flowers. The corresponding visitation rate for exposed plants is $(0.75 \times 0.33q) + (0.25 \times q)$. The ratio of the two rates reduces to $(0.50q/0.83q) = 0.60$, suggesting that visitation to exposed plants is only 60% as great as to protected ones. In our whole-plant observations, visitation to damaged plants was lower than predicted by flower-level responses. In 1994, visitation rates to all flower types on exposed plants were only 44% as great as on protected plants (Fig. 2b). The 95% confidence limits around this ratio are $\pm 0.16$, putting the upper limit right at the expected visitation rate. In 1995, visitation rates to flowers on exposed plants were only 25% as great as on protected plants (Fig. 2b). With the 95% confidence limits at $\pm 0.17$, this ratio is well below the expected 60%. These calculations support the hypothesis that pollinators respond to damage at the whole-plant level.

Pollinators may be responding at even higher organization levels to beetle damage, such as the mean and variance in damage within a local patch. In such a case, the reproductive success of a particular plant could depend not only on its own damage level, but also on that of its neighbors. Looking at Fig. 5, one can see that in 1994 the visitation rates to exposed plants in patches containing only exposed plants were 12% as great as visitation rates to protected plants in protected patches. By contrast, in mixed patches, visits to exposed and protected plants combined were 25% as great as visits to protected plants in protected patches. Approximately 22% of all the flowers in exposed patches were undamaged, compared to 43% undamaged flowers in mixed patches, and 87% undamaged flowers in protected patches. The corresponding expected visitation rates to the patches, as above, would be $(0.22 \times q) + (0.78 \times 0.33q) = 0.48q$ for exposed patches, $(0.43 \times q) + (0.57 \times 0.33q) = 0.62q$ for mixed patches, and $(0.87 \times q) + (0.13 \times 0.33q) = 0.91q$ for protected patches. Thus, the ratio of the rates for exposed vs. protected patches and for mixed vs. protected patches would reduce to 0.53 and 0.68, respectively. The observed respective rates of 12% and 25% are much lower than expected, suggesting that pollinators reject plants based upon neighborhood levels of beetle attack in addition to levels of individual flower damage.

Attack by floral herbivores can have an obvious direct effect on plant reproductive success by destroying pollen, ovules, and seeds. However, when pollen vectors are deterred by damage, surviving gametes can go unused. Thus, floral herbivores can have further indirect effects on reproduction, both through male function (pollen donation) and female function (pollen receipt). These potential indirect effects of floral herbivores have not yet received much attention. Murawski (1987) observed that butterfly pollinators avoided visiting infested *Psiguria warscewiczii* flowers after encountering tephritid fly larvae in the flowers. Similarly, Cunningham (1995) found a negative correlation between katydid damage and pollinating bat visitations in *Calyptrogyne ghiesbreghtiana*. In one previous experimental study, Karban and Strauss (1993) found that damaged *Erigeron glaucus* flower heads placed into artificial arrays were less likely to be visited by pollinators than undamaged flowers. In addition, insects generally respond negatively to asymmetric flowers, regardless of their being asymmetric by developmental constraints (Møller and Eriksson 1995) or by herbivore damage. We are not aware of any previous study that has employed field manipulations to measure the consequences of flower predation at natural levels for pollinator service. By using insecticide to inhibit natural flower predation, we found that herbivore attack in *I. arborea* damages flowers, reduces pollination re-

wards, diminishes the size of the floral display, and consequently decreases pollinator visitation.

In a companion paper (Krupnick and Weis 1999) we provide evidence that pollinator response to floral damage translates to a reduction in at least one component of male reproductive success. Furthermore, pistils on damaged plants received less pollen, creating a potential for reduced female success. However, seed set is not pollen limited in *I. arborea,* and so pollinator responses to damage do not appear to alter female reproductive success beyond direct herbivore damage. Thus, the consequences of herbivory for female plant fitness are not necessarily the same as those consequences for male plant fitness. Moreover, the results indicate that the indirect effects through pollinator activity have a greater effect on male reproductive success than on female reproductive success.

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