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Christopher J. Norment
The College at Brockport, cnorment@brockport.edu

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The Effect of Nectar-thieving Ants on the Reproductive Success of Frasera speciosa (Gentianaceae)

CHRISTOPHER J. NORMENT
Westover School, Middlebury, Connecticut 06762

ABSTRACT.—The impact of nectar-thieving ants on the reproductive success of Frasera speciosa (Gentianaceae), a perennial monocarp with periodic, synchronous flowering, was studied in a Wyoming alpine meadow. Plants from which ants were excluded had higher rates of flower visitation by other insects, and higher standing crops of nectar, than did plants visited by ants. However, there were no significant differences in either seed set or seed predation in plants with and without ants. The lack of effect of ants upon the reproductive success of Frasera may be due in part to temporal separation of the activities of ants and some important pollinators and seed predators. However, the abundant nectar production, large inflorescences and low rates of seed predation in Frasera, which are all related to its habit of periodic synchronous flowering, may reduce the effects of nectar-thieving ants upon the species.

INTRODUCTION

Ants that feed on floral nectar pollinate several temperate plant species, including Polygonum cascadense (Hickman, 1974), Oreoxis alpina, Eritrichium artemioides and Thlaspi alpestre (Petersen, 1977), and Diamorpha smallii (Wyatt, 1981). However, ants may also act as nectar robbers or thieves (McDade and Kinsman, 1980; Willmer and Corbet, 1981; Schaffer et al., 1983), thus decreasing floral rewards without contributing to pollination. Nectar-robbing or -thieving ants (sensu Inouye, 1980) may reduce the reproductive success of the plants they visit. Inflorescences of Asclepias curassavica from which ants were excluded showed higher rates of pollinia insertion than did inflorescences visited by ants (Wyatt, 1980). Umbels and stems of Asclepias syriaca visited by ants initiated fewer pods than did umbels and stems without ants (Fritz and Morse, 1981). In a study of Pavonia dosypetala, flowers robbed by both bees and ants produced fewer seeds than flowers visited only by pollinating hummingbirds (Roubik, 1982). Galen (1983) found that nectar-thieving ants decreased seed production in Polemonium viscosum, a perennial alpine herb of western North America, by damaging the gynoecium during nectar foraging. Ants may also decrease reproductive success by impairing pollen function (Beattie et al., 1984). With few exceptions (Fritz and Morse, 1981; Fowler and Whitford, 1982; Galen, 1983), most studies of nectar-robbing and -thieving ants have occurred in tropical regions. In this article I examine the impact of nectar-thieving ants upon the reproductive success of monument plant (Frasera speciosa) (Gentianaceae), a long-lived perennial monocarp that grows in montane regions throughout western North America (Beattie et al., 1973). Specifically, I: (1) quantify ant visitation to Frasera flowers; (2) measure the impact of ants upon pollinator visitation and nectar resources and (3) examine the effect of ants upon seed set and seed predation.

Frasera speciosa exhibits a pattern of synchronized flowering in which large amounts of elongated flowering stalks up to 3 m high are produced at 2-4-yr intervals (Beattie et al., 1973; Taylor and Inouye, 1985). Each inflorescence contains hundreds of campanulate-rotate, 2-5 cm broad, flowers. A large nectary, consisting of two canals up to 1 cm long, with fimbriate margins, is located at the base of each corolla lobe. Frasera flowers attract a
large variety of pollen- and nectar-feeding insects, including coleopterans, dipterans, hymenopterans and lepidopterans (Beattie et al., 1973).

METHODS

Ant–Fraser interactions were studied between 1 July–20 August 1984 in an alpine meadow (elevation 3050 m) at Clay Butte in the Beartooth Mountains, Wyoming. In 1984, Fraseria inflorescences were very abundant, and plants flowered between 4 July–15 August. Twelve pairs of plants were selected for intensive observations; ants were excluded from one member of each pair by coating the base with Tanglefoot®, tying up enough rosette leaves to prevent ant access (ca. four out of a minimum of 30 leaves) and clipping surrounding vegetation. Since Fraseria exhibits density-dependent seed set (Taylor and Inouye, 1985), plants were selected so that members of each pair were within 2 m of one another.

At 3-d intervals, 5-min censuses of flower visitors were conducted on each plant. Immediately prior to observing each plant, I counted all ants on the inflorescence. During each census the number and type of all flower visitors except ants were recorded. Subsequent identification of specimens from a reference collection of Fraseria visitors allowed most insects to be identified to the genus or species level (Table 1), although common dipterans could not be identified beyond the order level while in the field. In addition to counting flower visitors, I also tallied all ant–flower visitor interactions in which an ant caused a foraging insect to leave a flower.

Fraseria plants in the study population flowered from 4 July–15 August, but to simplify comparisons between treatments and individuals, data on visitation were gathered during the 3-wk period when all stalks contained open flowers. Each plant was censused seven times; total observation time for each treatment was 420 min. To determine seed set and seed predation, 50 mature ovaries were collected randomly from all portions of each plant, preserved in 70% ethanol, and later dissected. Values for the proportion of seed set and fruits damaged per plant were arcsin-transformed to correct for nonnormality before statistical analysis.

An exclusion experiment was conducted to determine the effects of ants upon standing crops of nectar. On each of four sampling dates, all flower visitors were excluded from three plants near those used in the visitation experiment by coating the base of the flowering stalk with Tanglefoot® and enclosing the entire inflorescence in a fine-meshed nylon bag. At the same time, the stalks of three adjacent plants were covered with the same material staked to the ground; this prevented visits by flying insects, but allowed free access by crawling insects. After 24 h, six flowers were collected from each inflorescence and their nectar volumes measured to the nearest 0.1 μl with a microsyringe. Nectar concentrations (total dissolved solids) were measured with a hand refractometer immediately after collection of samples from flowers with total accumulations of ≥10 μl.

RESULTS

The most common visitors to both ant-access and ant-exclusion plants were small dipterans (primarily Muscidae and Bibionidae), a small nectar-gathering bee (Evylaeus synthridis) and a nectar-feeding elaterid beetle (Ctenicera fallax) (Table 1). Workers of two bumblebee species (Bombus centralis and B. frigidus) were observed occasionally; a noctuid moth (Euxoa levisit) was found on plants in both treatments, although it was not seen during the timed censuses. An average of 34.4 ± 27.8 (SD) ants/plant, primarily Formica neorufibarbis, were counted on ant-access plants. These ants were active mainly around floral nectaries and rarely contacted stigmas or anthers. Heights and number of flowers per inflorescence did not differ significantly between ant-access and ant-exclusion plants (Table 2).
Table 1.—Flower visitors to ant-access and ant-exclusion *Frasera* speciosa plants during timed censuses at Clay Butte

<table>
<thead>
<tr>
<th>Order/family</th>
<th>Visitors</th>
<th>Number of observations/treatment&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Ant-exclusion</td>
</tr>
<tr>
<td>Hemiptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miridae</td>
<td>?</td>
<td>3</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cerambycidae</td>
<td><em>Cortodera subpilosa</em></td>
<td>12</td>
</tr>
<tr>
<td>Elateridae</td>
<td><em>Ctenicera fallax</em></td>
<td>43</td>
</tr>
<tr>
<td>Diptera&lt;sup&gt;b&lt;/sup&gt; (includes Anthomyiidae, Bibionidae, Empididae, and Muscidae)</td>
<td></td>
<td>619</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Noctuidae</td>
<td><em>Euxoa lewisi</em></td>
<td></td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andrenida</td>
<td><em>Andrena sp.</em></td>
<td>2</td>
</tr>
<tr>
<td>Apidae</td>
<td><em>Bombus frigidus</em></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Bombus centralis</em></td>
<td>4</td>
</tr>
<tr>
<td>Chrysididae</td>
<td><em>Chrysis</em></td>
<td>1</td>
</tr>
<tr>
<td>Formicidae</td>
<td><em>Formica neorufibaris</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Formica sp. (fusca group)</em></td>
<td></td>
</tr>
<tr>
<td>Halictidae</td>
<td><em>Evylaeus synthridis</em></td>
<td>118</td>
</tr>
<tr>
<td>Ichneumonidae</td>
<td>?</td>
<td>10</td>
</tr>
<tr>
<td>Sphicidae</td>
<td><em>Crabro</em></td>
<td>3</td>
</tr>
<tr>
<td>Tenthredinida</td>
<td><em>Tenthredo erythromera</em></td>
<td>5</td>
</tr>
<tr>
<td>Total visitors</td>
<td></td>
<td>822</td>
</tr>
</tbody>
</table>

<sup>a</sup> Numbers equal sums of all flower visitors counted during the observation period of seven censuses

<sup>b</sup> Some Diptera was not identified past the order level

<sup>c</sup> Not observed during timed censuses

Mean number of flower visitors/plant was significantly lower on ant-access plants than on ant-exclusion plants (Table 2). During the censuses, ants foraging on *Frasera* nectar were observed chasing visitors from flowers 48 times. Ants only displayed aggressive behavior towards smaller insects, such as dipterans and solitary bees; larger visitors (*Bombus* and *Ctenicera*) were ignored.

Nectar standing crops were significantly greater (t = 6.66, P < 0.001) in ant-exclusion plants (\( \bar{x} \pm SD = 6.31 \pm 2.28 \mu l, n = 72 \)) than in ant-access plants (\( \bar{x} \pm SD = 2.28 \pm 2.82 \mu l, n = 69 \)). Nectar concentrations were similar in flowers collected from ant-exclusion plants (\( \bar{x} \pm SD = 42.3 \pm 6.8\% , n = 38 \)) and ant-access plants (\( \bar{x} \pm SD = 36.5 \pm 8.6\% , n = 14 \)). Although all flowers collected from ant-exclusion plants had nectar, 14 (20.3\%) of the flowers from ant-access plants were without measurable nectar accumulations. In addition to reducing nectar standing crops, ants also damaged the nectaries by chewing off the fimbriate margins of the nectar-producing canals. All ants collected from *Frasera* flowers and later examined in the laboratory (n = 30) were without detectable pollen on their bodies.

Proportion of seed set varied from 0.085 to 0.724 in ant-access plants, and 0.083 to 0.689
in ant-exclusion plants. The proportions of mature ovules were not significantly different in fruits collected from plants with ants and those without ants (Table 2). For ant-access plants, there was no correlation \((r = 0.197, P > 0.05)\) between the average number of ants seen on a plant and seed set.

Larvae of an unidentified geometrid moth that fed on developing seeds were found at low levels in the fruits of both ant-access and ant-exclusion plants. There was no significant difference between the proportion of parasitized fruits in the two treatments (Table 2).

**DISCUSSION**

The types of flower visitors on *Frasera* plants at Clay Butte were similar to those listed by Beattie *et al.* (1973) for Colorado populations, although ants and beetles were less common and *Bombus* were more abundant, than in the present study. In addition, the geometrid moth larva found in *Frasera* ovaries at Clay Butte differs from previously described seed predators, which include a tortricid moth and agromyzid fly (Beattie *et al.*, 1973; Taylor and Inouye, 1985).

Ants were frequent visitors to flowering stalks of *Frasera* in the Clay Butte population, and fed heavily on floral nectar. Results of the ant-exclusion experiments showed that plants visited by ants had lower standing crops of nectar, and lower rates of visitation by other arthropods, than did plants from which ants were excluded. Thus it is surprising that ants had no measurable impact on either seed set or seed predation in the population.

There are several possible explanations why ants did not affect seed set. First, ants at Clay Butte are active during the day (pers. observ.), and would have little effect on nocturnal pollinators. Nocturnal moths were found on many *Frasera* plants at Clay Butte; in Colorado, they may play an important role in pollination, and in some years are more common on *Frasera* flowers at night than *Bombus* are during the day (D. W. Inouye, pers. comm.). Since the major seed predator on Clay Butte *Frasera* is a geometrid moth, lack of nocturnal activity by ants would also explain the similar seed predation rates in ant-access and ant-exclusion plants. Second, traits associated with periodic synchronous flowering in *Frasera* may mean that seed set generally is limited neither by pollination nor seed predation, thus reducing or eliminating potential effects of nectar-thieving ants. *Frasera* populations suffer little predation (<5%) at high flowering densities (Beattie *et al.*, 1973; Taylor and Inouye, 1985; present study), and the large inflorescence, and abundant, easily obtainable nectar may promote maximum floral visitation during periodic flowering, when *Frasera* attracts a
greater diversity and number of pollinators than do sympatric species (Beattie et al., 1973). Abundant nectar production would also help compensate for losses to nectar-thieving ants, and ensure that sufficient accumulations remain to attract pollinators.

An alternative hypothesis, that ants positively affect reproductive success by increasing pollen dispersal, is unlikely. Although *Formica neorufibarbis*, which visits *Frasera* at Clay Butte, may pollinate several alpine plants in Colorado (Petersen, 1977), *Frasera* does not possess the vegetative or floral characteristics common to plants having the "ant pollination syndrome" (Hickman, 1974; Petersen, 1977), which include a short or prostrate growth form and small sessile flowers that have few seeds and minimal nectar rewards. There are many exceptions to the ant pollination syndrome (Beattie, 1985), but the large, campanulate-rotate form of *Frasera* flowers, and the distance between the nectararies and anters (see Beattie et al., 1973) makes it unlikely that ants will pick up pollen while foraging for nectar. Furthermore, no traces of *Frasera* pollen were found on the bodies of ants collected at Clay Butte. Since foraging ants rarely contact dehiscing *Frasera* anters, it is also unlikely that they would negatively affect pollen viability, as has been shown for some species (Beattie et al., 1984). Finally, although nectar thieves may sometimes promote outcrossing by increasing pollinator movement among flowers (Heinrich and Raven, 1972), the absence of increased seed set in ant-access plants suggests that ants do not have this effect on pollen flow in Clay Butte *Frasera*.

Beattie (1985) proposed that most ant–plant mutualisms evolve in response to stress selection on plants. Periodic synchronous flowering, which almost eliminates *Frasera* as a prey item in most years, may result in low rates of seed predation, as well as improving the ability of *Frasera* when in flower to attract a wide variety and number of pollinators. Presumably, these effects would remove any selective advantage for the evolution of mutualistic relationships involving either pollination or predation. Given the flowering strategy of *Frasera*, it is difficult to see how plant fitness would be increased by allocating resources to attract ant protectors or pollinators, or how ants would benefit by specializing on the species.

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Literature Cited


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