

**Protection at a price? Ant interactions with pollinators on  
aspen sunflower (*Helianthella quinquenervis*)**

**Joshua M. Davendonis**

**Mentor: Sean Menke**

**Structured Undergraduate Research Program**

**Rocky Mountain Biological Laboratory**

**P.O. Box 519**

**Crested Butte, CO 81224**

**ABSTRACT** The purpose of extrafloral nectar secretion in the aspen sunflower, *Helianthella quinquenervis* (Asteraceae), has been previously explained as mediating a number of facultative plant-ant mutualisms, through which the plant is protected from seed- parasitizing flies. The current study tested the hypothesis that extrafloral nectar production in the aspen sunflower maximizes ant protection from herbivores while minimizes their interactions with pollinators. Additionally, we were interested in the importance of ant community composition and how altering ant abundances would affect the relationship between ants, herbivores, and pollinators on the aspen sunflower. Despite a twofold increase in treatment-influenced ant abundance, we found that there was no effect of this on either herbivory or pollinator visits. This experimental evidence suggests that distraction, in addition to protection, may be a major reason for the existence of extrafloral nectar in this system.

*Key words: ant, distraction hypothesis, extrafloral nectar, Helianthella quinquenervis, mutualism, protection hypothesis*

## Introduction

Plant-ant mutualisms are common in a variety of different habitats (Inouye & Taylor 1979, Boucher et al. 1982). These mutualisms are context-dependent systems that involve a variety of species interactions and variable benefits for all partners (Morales 2000, Ness et al. 2006). Widespread plant-ant mutualisms often consist of a plant providing an energy resource and/or domatia for the ants which in turn serve as bodyguards by attacking herbivores and seed-predators/parasites (Inouye and Taylor 1979, Koptur 1984, Rudgers 2004). This indirect deterrence of natural enemies employed by plants is often mediated through the production of extrafloral nectar (EFN),

a process found in greater than 25% of angiosperms families (Bentley 1977, Rudgers & Gardener 2004, Chamberlain & Holland 2008).

Two hypotheses exist for the occurrence of extrafloral nectar. The protection hypothesis states that extrafloral nectar attracts arthropod predators, in many cases ants, which deter herbivores and seed predators/parasites (Bentley 1977). This hypothesis has also been used to explain the ant-homoptera interaction (Becerra & Venable 1989, Del-Claro & Oliveira 1993). Additionally, the distraction hypothesis states that the location of extrafloral nectaries relative to plant reproductive structures acts to distract flower-damaging ants or other visitors from flowers, and consequently pollinators as well (Wagner & Kay 2002, Galen 2005). It may be advantageous for plants to limit ant access to floral resources as ants do not usually act as pollinators and have also been identified in some systems as nectar robbers (Altshuler 1999, Wagner & Kay 2002). Though these hypotheses are not mutually exclusive, they represent two different perspectives on the relationship between plants and ants. In the event that ants receive floral resource rewards without benefiting the plant through pollination, the mutualism would breakdown, a notion that provides a support to the distraction hypothesis (Galen 1983, Wagner & Kay 2002).

Extrafloral nectaries are located either behind flowers or lower on a stalk or branch, which focuses ant activity in places separated from flowers (Inouye and Taylor 1979, Altshuler 1999, Wagner & Kay 2002). This manipulation of ant distributions reduces the likelihood of ant-pollinator interactions and serves as evidence for the previously mentioned distraction hypothesis (Raine et al. 2002). An ant's inability or failure to discriminate between herbivores, seed-predators/parasites, and pollinators

could result in a decrease in fitness for the host plant (Altshuler 1999, Ness 2006). For instance, studies on *Acacia hindsii* and *Ferocactus wislizeni* have demonstrated that the presence of ants on flower heads can interfere with plant-pollinator interactions and reduce pollinator visits with subsequent reductions in reproductive fitness (Raine et al. 2002, Wagner & Kay 2002, Ness 2006).

Unlike *Acacia hindsii* and *Ferocactus wislizeni*, it remains unknown if ants interact with pollinators on the aspen sunflower (*Helianthella quinquenervis*), a montane wildflower that secretes extrafloral nectar (Inouye & Taylor 1979). Aspen sunflower extrafloral nectar is secreted behind the flower head in the margins of the involucre bracts and foraged on by a number of ant species, the dominant group belonging to large bodied ants in the genus *Formica* (Inouye & Taylor 1979, S. Menke, *personal communication*). In their study of aspen sunflower ant recruitment, Inouye and Taylor (1979) found that proximity to *Formica* sp. nests was correlated with lower levels of seed parasitism. Additionally, observations of *Formica* sp. on aspen sunflowers reveal that these ants are highly aggressive and displace smaller, less aggressive ants foraging for extrafloral nectar (Inouye & Taylor 1979, Sean Menke, *personal communication*). While the aspen sunflower-ant system is well documented with respect to ant protection against seed-predators/parasites, the effect of ants on pollinator-plant interactions has not been rigorously investigated. However, Inouye & Taylor (1979) observed that ants tend to stay behind the flower head, near the extrafloral nectaries, and that extrafloral nectar was collected as quickly as it was produced. In addition D. Inouye (*personal communication*) has observed that extrafloral nectaries stop secreting once flower heads are ready for pollinators. These observations suggest that extrafloral

nectar production has been optimized to maximize protection from herbivores and seed parasites, and minimize interactions with pollinators.

The goal of this experiment is to determine how aspen sunflower extrafloral nectar mediates ant abundance as well as to quantify the relationship, if one exists at all, between ants and pollinators in this system. I quantified pollinator activity on the flowers and documented how these interactions changed if individuals of the dominant ant group were removed. Moreover, I attempted to determine which hypothesis best explains aspen sunflower extrafloral nectar production: the protection or the distraction hypothesis. In order to accomplish these goals, I performed a factorial study manipulating both extrafloral nectar availability and ant species occurrence in the aspen sunflower system. I tested the hypothesis that extrafloral nectar production in the aspen sunflower maximizes ant protection from herbivores while minimizes their interactions with pollinators. From this, I predicted that ants would not differentiate between herbivores, seed-predators/parasites, and pollinators in their defense of the aspen sunflower. Furthermore I expect that increasing ant abundance on the aspen sunflower by providing additional extrafloral resources would cause fewer and shorter pollinator visits. Additionally, I tested the hypothesis that different ant genera will have different effects on herbivore and pollinator-plant interactions. I predicted that excluding the dominant *Formica* sp. from the aspen sunflower would increase herbivory and the number and duration of pollinator visits

## Methods

*Helianthella quinquenervis* (Asteraceae), or the aspen sunflower, occurs in rocky meadows near patches of aspen (*Populus tremuloides*) in and around the Rocky Mountain Biological Laboratory, elevation 2871m. Flower heads of aspen sunflowers tend to emerge in early to mid-July based on elevation (Inouye 2008). Ants commonly seen foraging for extrafloral nectar on the flowers include species in four genera: *Formica*, *Tapinoma*, *Myrmica*, and *Lasius*. All four genera forage on the plants several weeks prior to flower head emergence and continue until flowering ceases and the flower heads wilt.

### Study Sites

Research sites were located near aspen stands in the rocky meadows on the west facing hill-slopes approximately 0.6 kilometers north of the Rocky Mountain Biological Laboratory between elevations 2927-2946m. Twenty plots were randomly assigned to patches of aspen sunflowers as they occurred in the meadows.

### Extrafloral Nectar Production Manipulation

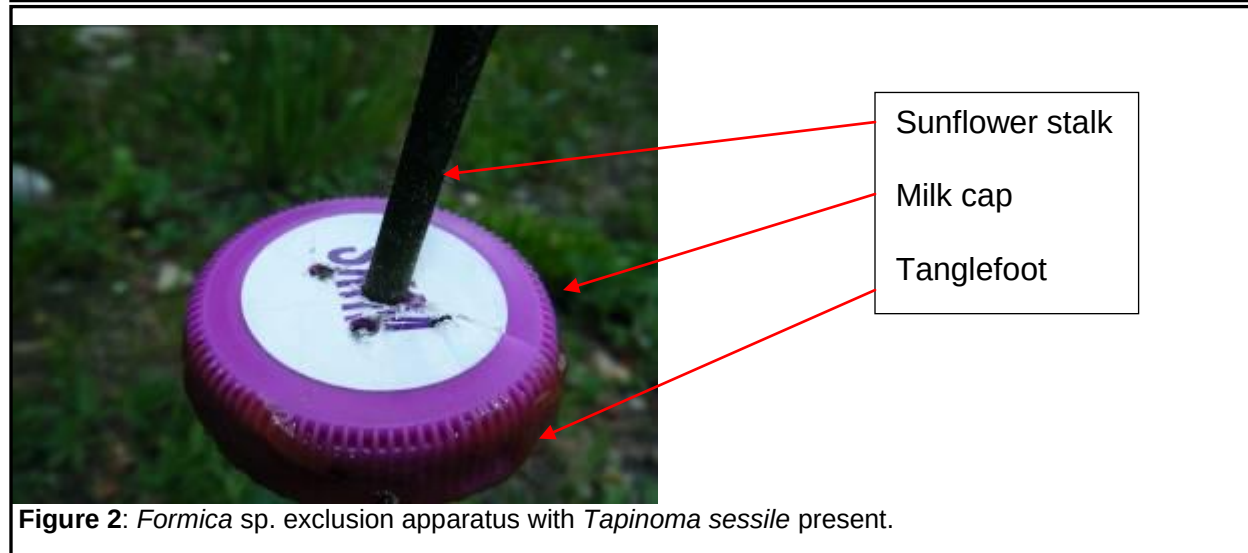
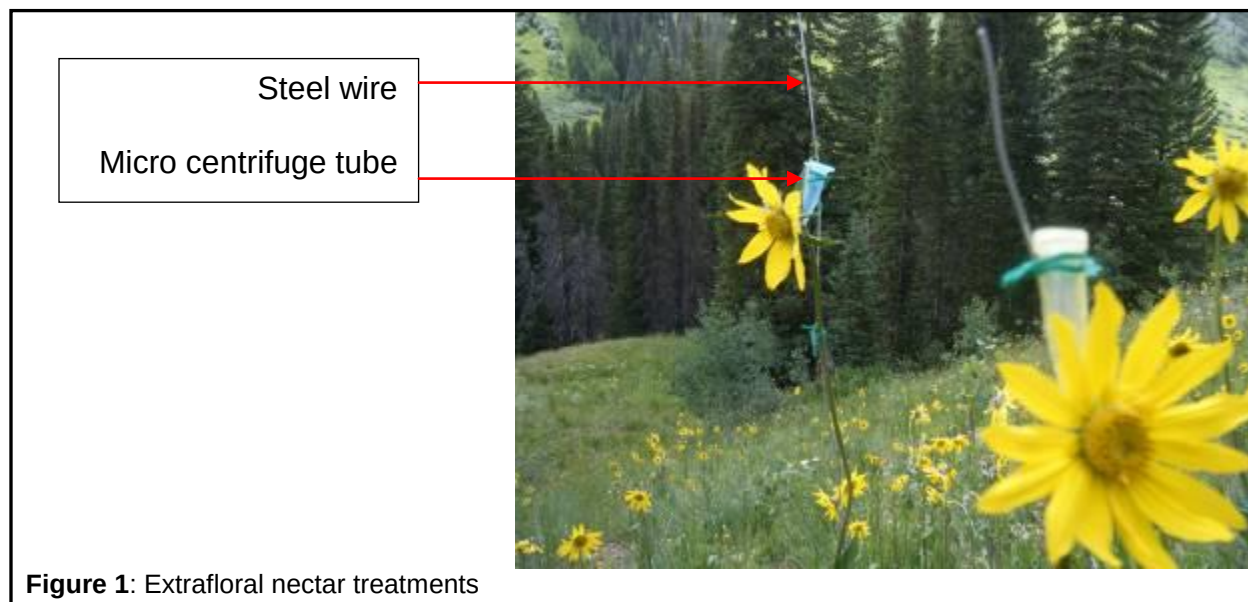
In order to determine the effect of extrafloral nectar on ant abundance, I provided ants with an additional 15% honey in water solution. This extra resource mimics additional production of extrafloral nectar. Furthermore, a honey in water solution was chosen based on Inouye and Inouye's (1980) findings that aspen sunflower extrafloral nectar is especially rich in amino acids. A small hole, (0.16 cm in diameter) was drilled using a drill bit at the bottom of a two mL centrifuge tube so that ants were able to gain access to the solution. I placed the centrifuge tube behind the flower head at the

margins of the involucre bracts where extrafloral nectar is secreted to mimic an increase in extrafloral nectar availability. The centrifuge tube was attached to a 17 gauge steel wire with twist ties, which was in turn twist-tied to the stalk of plant (Figure 1).

### Restriction of Ant Access

To assess the importance of ant abundance and species composition to herbivory and pollinator visitation I also manipulated ant access to aspen sunflowers. One treatment completely restricted ant access to the sunflower through the application of Tanglefoot (Grand Rapids, MI, USA) around the stalk. A second treatment excluded the large dominant *Formica* sp. at the sites. This treatment, demonstrated in Figure 3, consists of a plastic milk jug cap (3.5cm in diameter) with 0.80 cm holes drilled through the top. These holes are small enough to deny larger *Formica* sp. access while large enough to allow smaller, less aggressive ant species passage. Tanglefoot was applied to the edge of the milk jug cap to prevent ants from climbing over the side. In order to account for the potential effect of the steel wire, all experimental stalks received steel wire attachments. Additionally, all leaves and other material from neighboring plants that come in contact with the experimental sunflower stalk above the treatment application were removed to prevent their use as a bridge by ants.

During the weeks before the flower heads emerged, I applied treatments to each of the sunflower stalks. This included application and maintenance of Tanglefoot, *Formica* sp. exclusion apparatuses, and additional extrafloral resources. Weekly treatment reapplication and daily plot maintenance were required to ensure that extrafloral nectar levels and removal treatments remained effective.



### Experimental Design

Manipulations of extrafloral nectar and ant abundance were combined in a factorial experiment (Table 1). Each treatment was applied to individual aspen sunflowers in a randomized-block design across 20 blocks for a total of 100 plants.

| <b>Extrafloral (EFN) Treatments/Ant Treatments</b> |
|----------------------------------------------------|
| EFN sugar addition + <i>Formica</i> exclusion      |
| EFN sugar addition + control                       |
| Control + <i>Formica</i> exclusion                 |
| Control + total ant exclusion                      |
| Control + control                                  |

**Table 1:** Experimental Treatments

Plant growth rate, condition (e.g. flower head emergence and number, leaf number and damage, flower head wilting and number), and ant abundance, and non-ant arthropod visitation were measured weekly for three weeks for each aspen sunflower plant from 9-22 July. Growth rate was measured as the change in height from the top of the terminal flower to the ground. Leaf damage was measured by counting the number of herbivore-induced holes present in the leaves.

Ant species abundance on each plant was recorded as the number of each ant species on the plant during a 30 second recording period in the morning (0800-1000h) and afternoon (1200-1600h). Counts were recorded twice a week for three weeks from 11-23 July. Voucher specimens of each ant species were collected for identification and deposited in the RMBL collection.

Starting on July 16 when flower heads began to emerge, observations of pollinator activity were made for ten-minute intervals between 0900 -1200h and 1300-1600h for eight days from 16-24 July. At the conclusion of the observational component, flower heads were collected to allow for seed set counts as an evaluation of aspen sunflower reproductive fitness relative to treatment application.

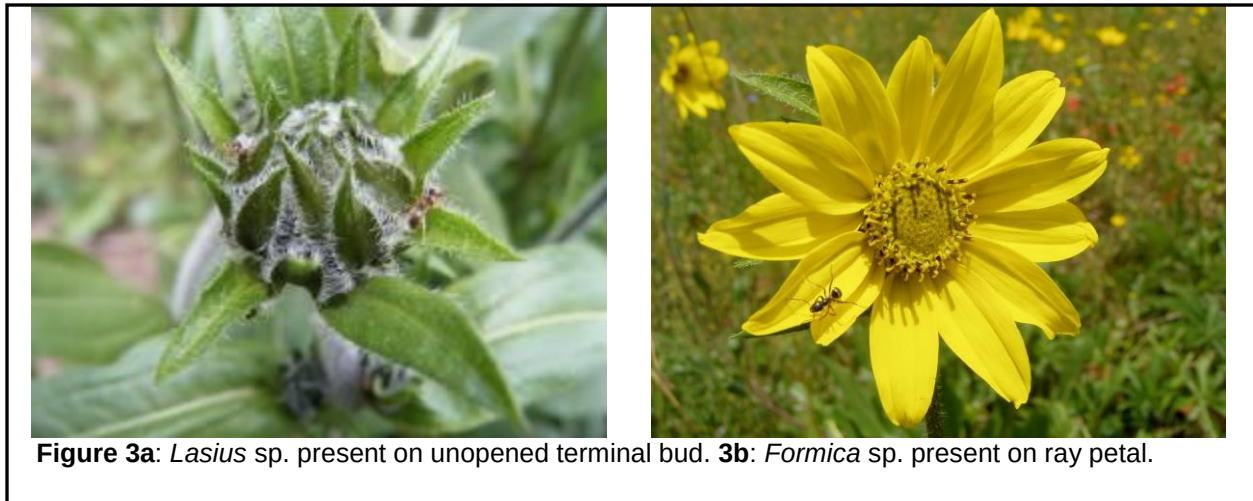
## Statistical Analyses

Analyses of Variance (ANOVA) as well as nonparametric Tukey-Kramer HSD comparison tests were used to detect differences between treatments with respect to the measured variables listed above using JMP software (SAS Institute, Cary, NC, USA). Manipulated independent variables were mean ant abundances averaged over three weeks and dependent variables were plant growth rate, leaf number and the difference in leaf damage, condition of the flower heads, and mean pollinator visits. Mean ant abundance data were log-transformed to account for non-normal distributions.

## **Results**

### Initial Observations

Earlier in the summer growing season, I observed six ant species: *Formica aserva*, *Formcia lasioides*, *Lasius neoniger*, *Lasius pallitarsis*, *Myrmica fracticornis*, and *Tapinoma sessile*, occurring on the unopened aspen sunflower buds despite the fact that no extrafloral nectar was present (Figure 3a). As flower heads began to emerge, I observed ants trailing on stalks, leaves, and both terminal and axillary involucres. While ants tended to remain near the bracts, many were observed traveling across the flower disc (Figure 3b).



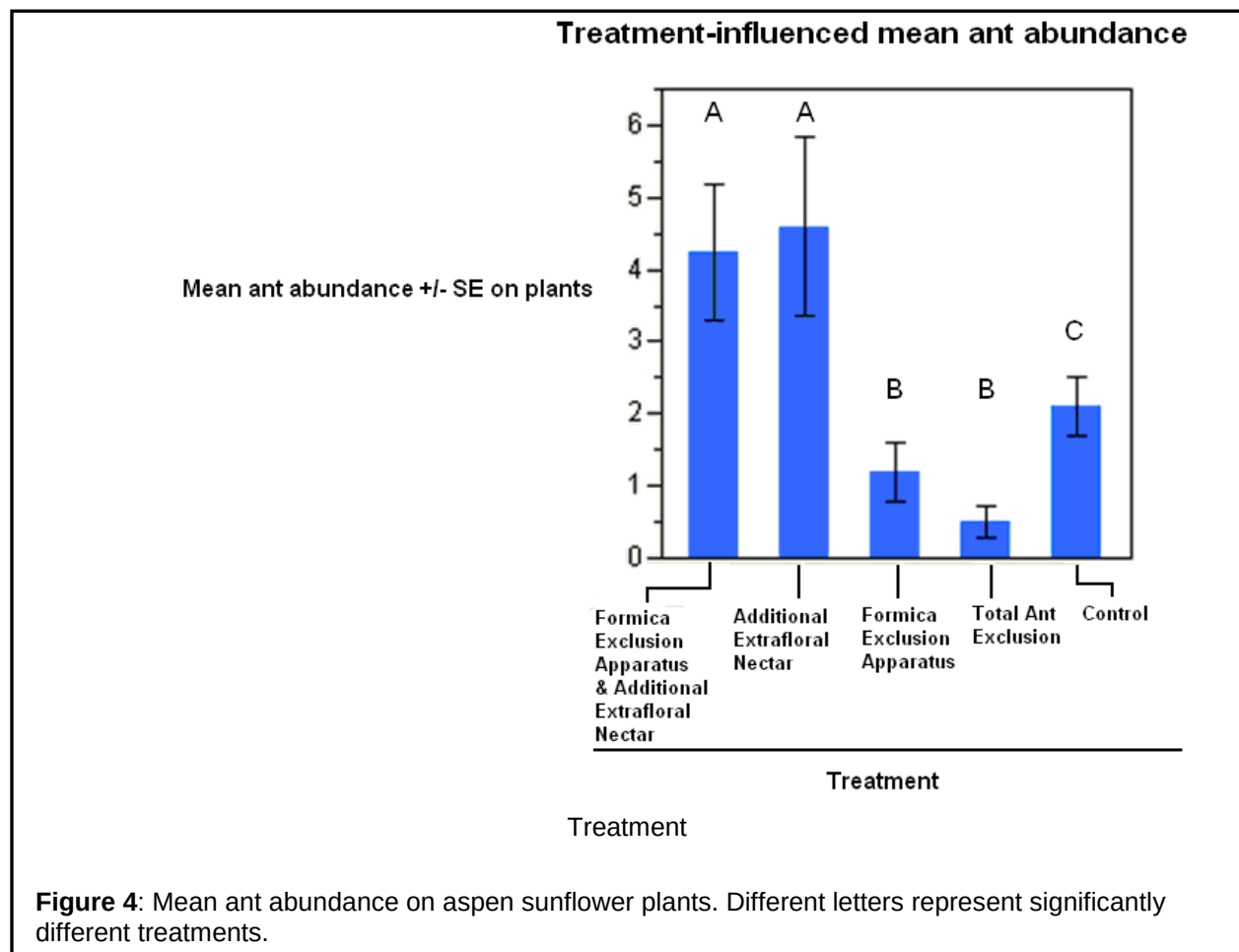
### Treatment Effectiveness

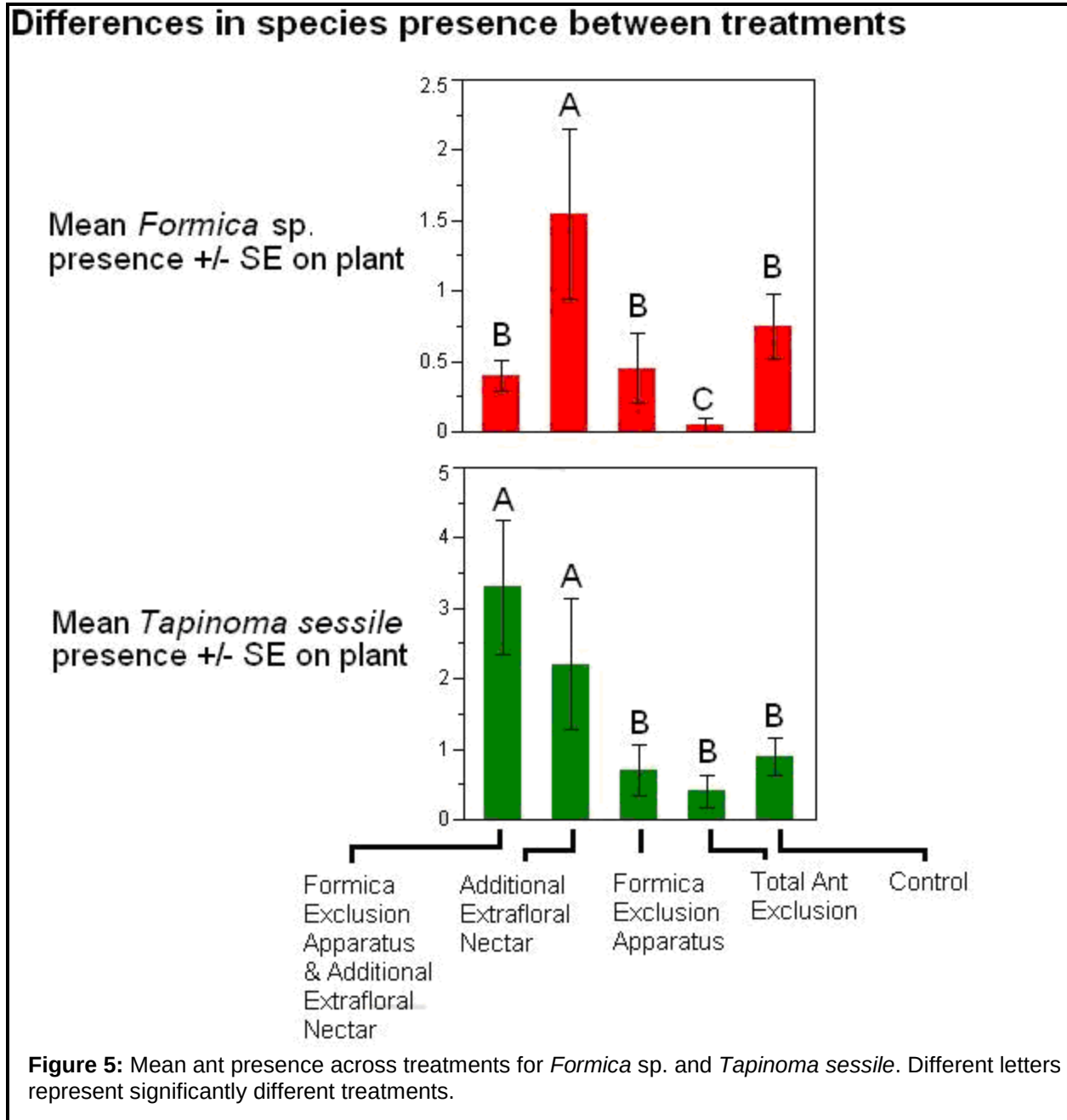
Experimental treatments had a significant effect on the mean ant abundance on aspen sunflowers by increasing the number of ants on extrafloral nectar addition / *Formica* exclusion and the extrafloral nectar treatments (ANOVA:  $F_{4,99} = 5.8981$ ,  $P = 0.0003$ , Figure 4). Additionally, the total ant exclusion and *Formica* exclusion treatments significantly reduced the number of ants present. (ANOVA:  $F_{4,99} = 5.8981$ ,  $P = 0.0003$ , Figure 4). The Tukey-Kramer HSD comparison test demonstrated that the extrafloral nectar addition / *Formica* exclusion and the extrafloral nectar treatments had more ants than the control plots (Figure 4). Additionally, *Formica* exclusion and total ant exclusion had the fewest numbers of ants.

There were also differences detected among treatments in the numbers of *Formica* sp. and *Tapinoma sessile* present on aspen sunflowers (ANOVA:  $F_{4,99} = 3.2495$ ,  $P = 0.0152$  and  $F_{4,99} = 3.6633$ ,  $P = 0.0081$ , respectively, Figure 5). Results of the Tukey-Kramer HSD comparison test show that *Formica* sp. were most abundant on plants with additional extrafloral nectar and least abundant on plants with total ant

exclusion treatments (Figure 5). Likewise, *Tapinoma sessile* were most abundant on plants treated with extrafloral nectar addition / *Formica* exclusion while least abundant on *Formica* exclusion apparatuses and total ant exclusion (Figure 5).

Though *Formica* exclusion apparatuses did not significantly decrease the overall number of *Formica* sp. workers on aspen sunflowers, they did succeed in excluding all individuals of one of the most aggressive species, *Formica aserva*.





### Growth

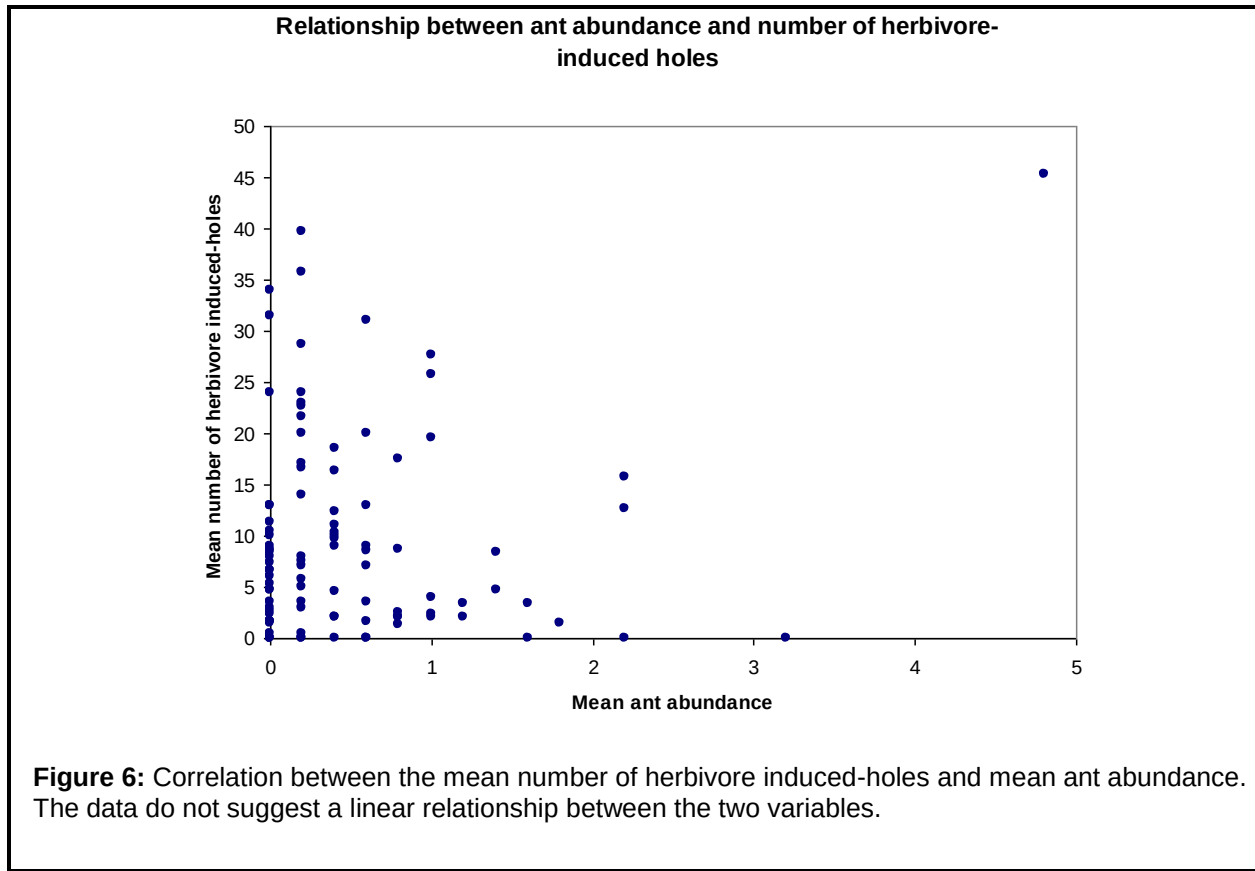
After three weeks, aspen sunflower growth across all treatments ranged from 1-29cm while plants gained a mean height of 6.7cm. However, there was no relationship detected between aspen sunflower growth and treatment application. Furthermore, there was no significant effect of ant abundance on aspen sunflower growth rates.

### Terminal and Axillary Flower head Emergence

The first terminal flower head emergence survey, performed on 9 July, revealed that 68% of terminal flower heads had emerged. Six days later on 15 July, all terminal flower heads had emerged. During the three week period of data collection, 54% of all terminal flower heads were consumed by macro-herbivores, the likely candidates being deer. ANOVA analysis produced no significant difference in the number of terminal flower heads eaten among experimental treatments. Additionally, no detectable correlation exists between the number of axillary flower heads and ant abundance, which was log transformed to account for nonrandom distributions.

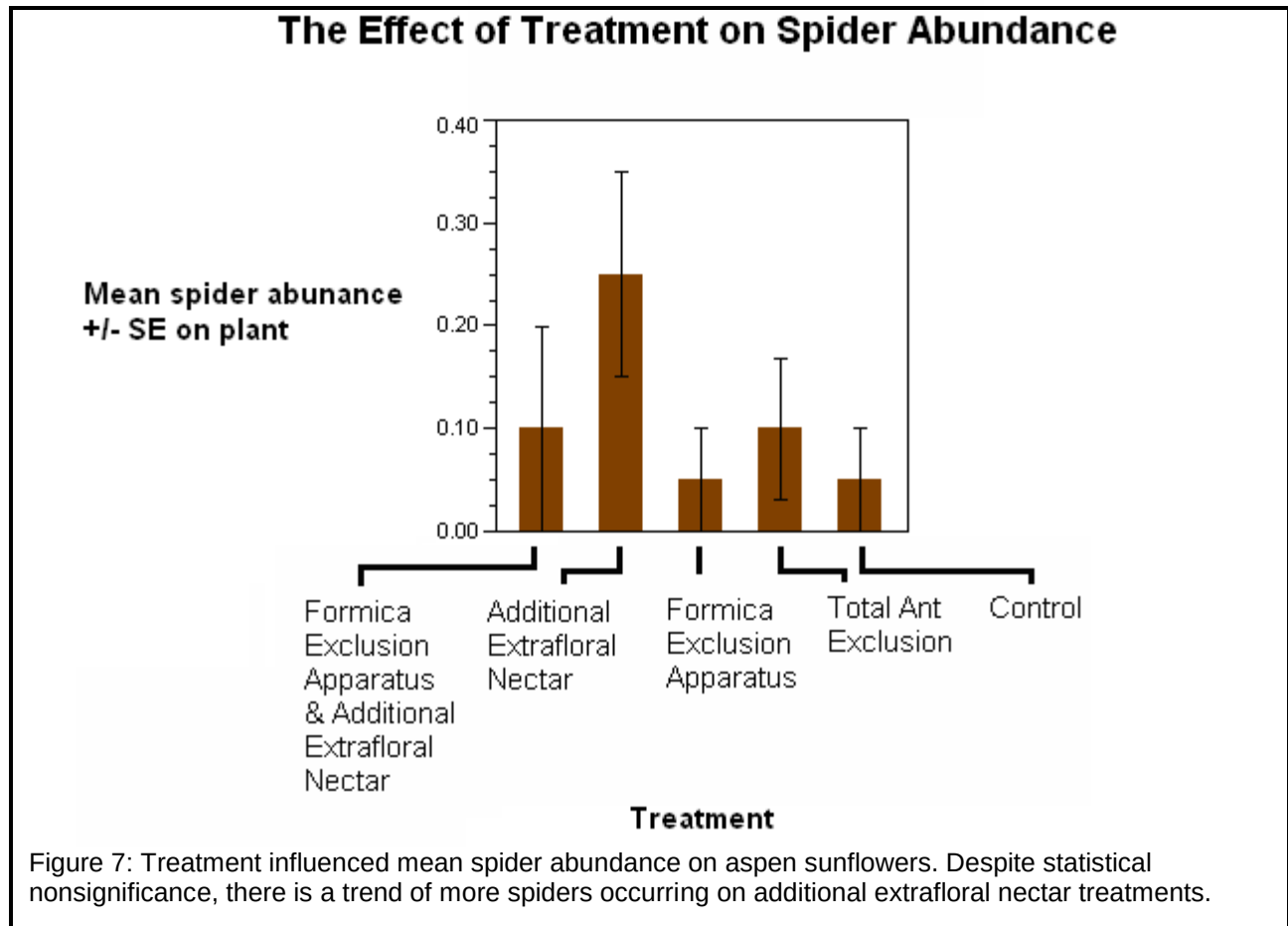
### Cauline Leaf Damage

The cauline leaves, those on the stem of the plant, of almost every experimental aspen sunflower experienced herbivory by arthropods. Only 6% of the plants were left untouched. Despite this widespread herbivory, there was no detectable difference in the number of cauline leaves damaged or the mean number of herbivore-induced holes among plants of different treatments. Similarly, there was no significant correlation between the abundance of ants present on the aspen sunflowers and herbivore-induced cauline leaf damage ( $F_{1,99} = 1.5913$ ,  $P = 0.2101$ , Figure 6).



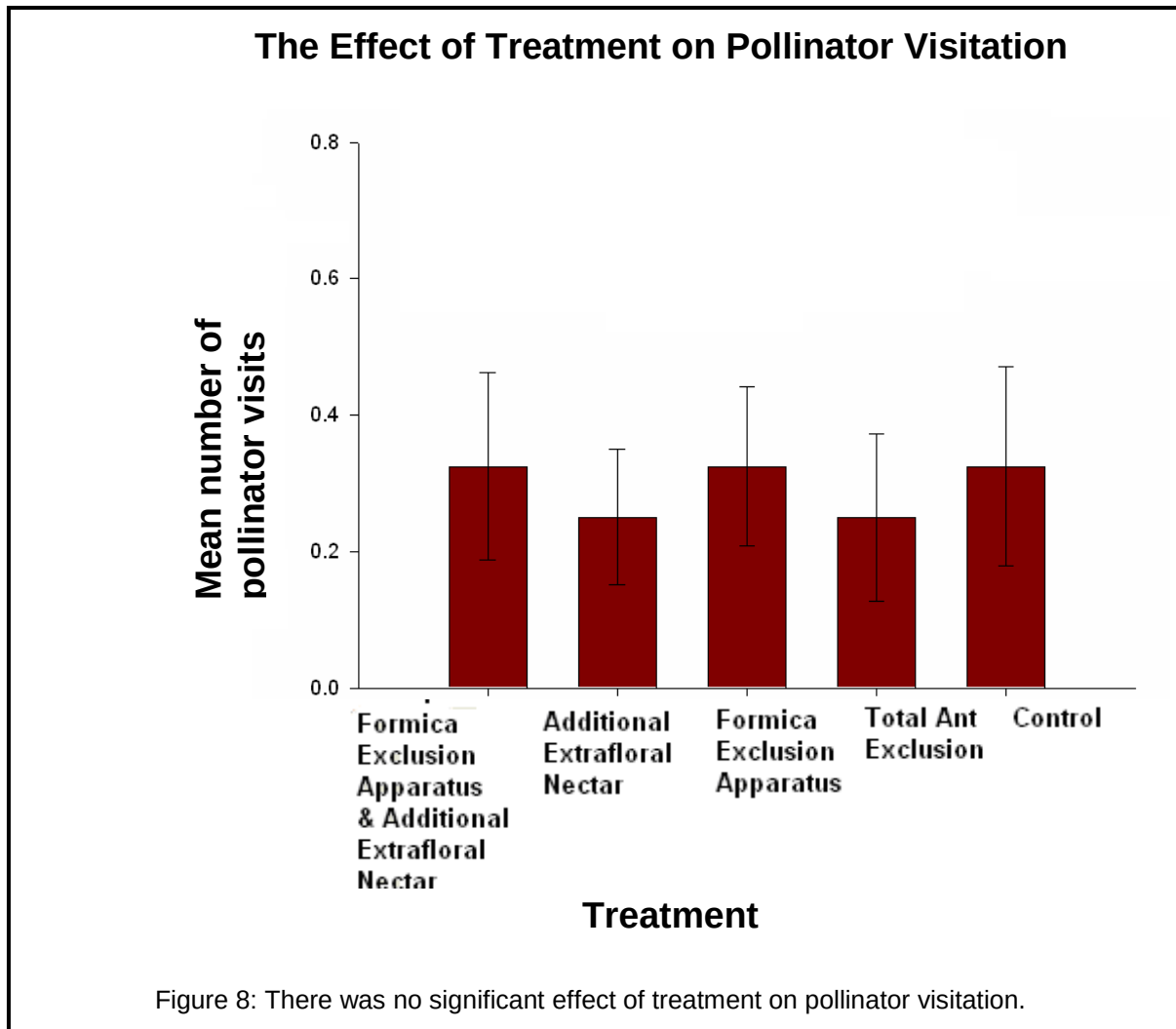
### Non-ant Arthropod Visitation

While performing ant abundance observations, I also recorded the number of non-ant arthropod visits to aspen sunflowers. I placed these visitors in two categories: spiders and tephritid flies. In total I observed 20 spiders and 11 tephritid flies across all treatments. When compared to log-transformed ant abundance, no correlation was detected. However, an ANOVA testing the effect of treatment on mean spider abundance revealed biologically significant trend of more spiders occurring on aspen sunflowers with additional extrafloral nectar ( $F_{4,99} = 1.14$ ,  $P = 0.3425$ , Figure 7).



### Pollinator Visitation

Five pollinator counts across eight days yielded 37 total pollinator visits to experimental aspen sunflowers. Despite one visit from an unidentified butterfly, all pollinators observed were bumblebees (*Bombus*). During a visit, a bumblebee would travel the entire length of the flower head edge and collect pollen. Though additional extrafloral nectar treatments effectively increased the number of ants present on the aspen sunflower, including the dominant *Formica aserva*, I never observed any interactions between ants and pollinators and there was no significant correlation between ant abundance and pollinator visitation. There was also no significant effect of treatment on pollinator visitation (ANOVA:  $F_{4,99} = 0.1072$ ,  $P = 0.9798$ , Figure 8)



## Discussion

In this study we strove to quantify the relationship between ants and aspen sunflowers as mediated by production of extrafloral nectar on pollinators and herbivores. In this particular system, I found that the extrafloral nectar production is crucial in mediating ant abundance, but ant abundance appears to play only a limited role in pollinator and herbivore interactions on with the aspen sunflower. I observed the entire spectrum of aggression, bound on one end by the smaller and more timid *Tapinoma sessile* and occupied on the opposite end by larger and belligerent *Formica*

*aserva*. Regardless of the variation of ant species composition or abundance, the lack of change in pollinator activity and herbivory is a compelling find given the body of literature concerned with the importance of ants involved in protective plant-ant mutualisms.

Temporal variation was observed in overall ant activity throughout the day. The plots, located on exposed west-facing hill slopes, received direct sunlight from 0900h until the sun set at approximately 2030h. Generally in the afternoon I observed limited ant activity on aspen sunflowers as ground temperatures were often too hot. Additionally, pollinator activity with respect to aspen sunflowers appeared to exhibit a similar decline from the period of 1300-1600h.

Caterpillar and other leaf-herbivore activity was rarely observed, though it clearly occurred throughout the day as evidenced by the fact that 96% of experimental aspen sunflowers experienced cauline leaf damage. There was concern at the onset of the study that the use of Tanglefoot around the stalk would completely eliminate leaf-herbivores along with ants. However, only one out of twenty aspen sunflowers that received this treatment did not experience herbivory on this scale.

Arthropod herbivory was not the only form of destruction to plants. Larger herbivores, most likely deer or elk, exacted widespread grazing of flower heads across all plots. These herbivores demonstrated no preference for any treatment applied to the experimental sunflowers and consequently consumed more than half of the terminal flower heads in the study over the course of three weeks. Not only were the herbivores not deterred by a steel wire extending above the plant, but in a number of instances, the centrifuge tube holding the honey water solution was eaten as well.

Seed-parasitizing flies, members of the family *Tephritidae*, were common non-ant arthropods observed on the flowers of *Helianthella*. In a period of three weeks, 20 flies were observed on the flower heads, cauline leaves, and stalks. Interestingly, I only observed pugnacious behavior towards a fly once by the very aggressive *Formica aserva* on an aspen sunflower treated with additional extrafloral nectar. Not only did it attempt to drive away the fly, but it also drove away a *Myrmica* sp. cohabitating the plant as well. This trend is held up the twofold increase in mean abundance of non-aggressive *Tapinoma sessile* on *Formica* exclusion treatments. However, this antagonistic behavior towards other ants was rarely observed.

Although the defense of aspen sunflower extrafloral nectar by *Formica* has been investigated by Inouye and Taylor (1979) my results conflict with their findings with respect to seed-parasites. The additional extrafloral nectar treatment increased not only ant abundance on the aspen sunflower twofold, but also the dominant ant genus by a similar amount, and still no difference in statistical difference in spider, tephritid fly, or total non-ant arthropod occurrence was detected.

The outcome of comparing the aforementioned increased ant abundance to pollinator activity is striking as well. Despite doubling the abundance of ants on the aspen sunflower, no effect on pollinators was found. Though Inouye and Taylor (1979) found support for the protection hypothesis based on seed counts and observations of pugnacious ant activity, experimental evidence from the present study lends support to the distraction hypothesis. I originally predicted that increasing ant abundance would increase the likelihood of ants occurring on the flower head. However, this was not the case. The ants were completely distracted by additional food source, which was

spatially separated from the flower head, and consequently were unaware of seed-parasites and pollinators.

The distraction hypothesis, first proposed in 1878, appears to have been set aside by the ecological community in favor of protection hypothesis (Wagner and Kay 2002). Indeed, many studies on plant-ant mutualisms open with blanket statements concerning the prolific nature of protection mutualisms. Though both hypotheses could operate together, the distraction hypothesis is set apart from the protection hypothesis and usually tested when investigators are concerned with nectar-robbing or flower-damaging ants (Galen 2005). My results suggest a reconsideration of the distraction hypothesis in regards to plant-ant mutualisms, as the present study's findings support a non-mutualistic relationship between plants and ants, similar to the findings of Becerra & Venable (1989), which suggest that extrafloral nectar distracts ants from aphid-tending behavior in order to reduce their negative effects. Following this, it seems the pressures that shaped the evolution of extrafloral nectar production in aspen sunflowers did not arise from a need to hinder herbivory and parasitism, but rather from a need to satiate exploitative ant species.

In order to determine if a more streamlined synthesis of the protection and distraction hypotheses is necessary to explain the plant-ant relationship in the aspen sunflower system, further research needs to be performed. The results of my study are not conclusive due to very small pollinator and herbivore counts. Additionally, longer observation times would most likely reveal ant-pollinator and ant-herbivore interactions that were undocumented because of time constraints. In the future, research in this area could be bolstered by focusing on experimental manipulation of herbivores along with

ants. Moreover, addressing the hypothesis concern requires more manipulation of extrafloral nectar production. It would be interesting to observe how ant-herbivore and ant-pollinator interactions would change if extrafloral nectar could be completely removed or if extrafloral nectar resources were placed on the face of the flower disc. In any case, my results serve as a springboard for future investigators hoping to further quantify how extrafloral nectar mediates these complex and varied species interactions.

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