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# Why eat extrafloral nectar? Understanding food selection by *Coleomegilla maculata* (Coleoptera: Coccinellidae)

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**Abstract** Methods of increasing predator abundance within a habitat include the incorporation of non-prey food items, yet the influence of this on predation intensity toward herbivores remains unknown. In order to gain an understanding of nectar feeding in the predaceous beetle, *Coleomegilla maculata* (DeGeer), laboratory studies were conducted evaluating prey consumption in the presence of extrafloral nectaries. The physiology of beetles with access to prey only and a mixed diet were compared. To elucidate results of beetle physiology, Y-tube olfactometer studies were conducted and preferences between food types evaluated. *Coleomegilla maculata* females consumed 9 % fewer aphids when nectar was available. Lipid and glycogen content, as well as oocyte volume were not increased upon consumption of a mixed diet. Evaluation of predator behavior when offered both food resources together and separately demonstrated that extrafloral nectaries are attractive.

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## Introduction

Despite efforts to place organisms into distinct feeding categories, investigation into dietary preferences has demonstrated that many arthropods are in fact omnivorous, consuming both prey and plant or fungal material (Lundgren 2009a; Coll and Guershon 2002). Omnivores have the ability to survive on multiple food classes (e.g., animal, plant, fungus, etc.), and this flexibility may serve to stabilize food webs (Fagan 1997; Lalonde et al. 1999; Coll and Guershon 2002; Singer and Bernays 2003). Fagan (1997) observed the ability of generalist predators, such as spiders, to control population outbreaks by switching prey items, dampening the effect of shifts in community composition. The consumption of plant resources by predators has implications for the outcome of biological control and predator conservation efforts (Coll and Guershon 2002; Lundgren 2009a). Natural enemies that can survive on non-prey resources are able to persist when prey is scarce, such as in the early spring in temperate climates prior to the build-up of prey populations (Lundgren 2009a). The incorporation of non-prey foods (e.g., sugar, pollen, fungi and plant material) into habitats may retain and promote predators despite a lack of insect prey (Landis et al. 2000). Specifically, incorporating sugar meals into the diets of

some predators often increases survival, reproduction, and nutrient reserves, particularly relative to unfed individuals (Lee and Heimpel 2008; Lundgren 2009b; Lundgren and Seagraves 2011). Diets comprised of both essential prey foods and sugar sources result in increased reproductive capabilities and adult performance in coccinellids (Lundgren 2009b). Many questions remain to be answered with regards to how omnivores focus their foraging efforts between prey and non-prey food items within a dynamic landscape (Eubanks and Denno 2000; Lundgren and Harwood 2012).

The predaceous capabilities of the Coccinellidae have made them a commonly studied group of predators (Obrycki and Kring 1998; Obrycki et al. 2009). In North America, *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) is a widespread, native, generalist predator that feeds on a variety of pest arthropods including aphids, mites, insect eggs and small larvae. Research evaluating the role of this predator in controlling economically damaging insects such as the European corn borer (Conrad 1959) and the Colorado potato beetle (Groden et al. 1990; Hazzard et al. 1991; Munyaneza and Obrycki 1998) has made this species a common focus of conservation biological control programs. Studies of dietary breadth indicate that predaceous Coccinellidae subfamilies are omnivorous, readily consuming sugar sources in the form of floral nectar, extrafloral nectar and honeydew, in addition to other plant-provided foods (Giorgi et al. 2009; Lundgren 2009a, b; Weber and Lundgren 2009). *Coleomegilla maculata* is no exception, as this species feeds on sugar from extrafloral nectaries (Lundgren and Seagraves 2011) and sucrose applied to crop plants (Seagraves et al. 2010). Incorporation of sucrose into agroecosystems has been investigated by introduction of diverse vegetation with nectaries, as well as the use of food sprays (Landis et al. 2000; Wade et al. 2008). Seagraves et al. (2010) observed significantly greater numbers of *C. maculata* in soybean plots treated with a sucrose food spray when compared to untreated plots, demonstrating the ability to increase numbers by incorporating sugar. Despite increasing predator abundance in treated plots, aphid numbers did not decline significantly. Understanding the interaction between prey and non-prey foods is essential to fully exploiting the attractive capabilities of sugar in agroecosystems.

A series of laboratory experiments were conducted to determine the relative physiological and behavioral effects of extrafloral nectar and the presence of aphid prey on *C. maculata* females. The objectives of this study were to examine the influence of nectar availability on *C. maculata* consumption rates of prey, pea aphids (*Acyrthosiphon pisum* Harris; Hemiptera: Aphididae), and determine how a mixed diet influences the physiology of females when compared with a prey-only diet. To provide insight into the physiological contributions of nectar to *C. maculata* fitness, a Y-tube olfactometer study was conducted to evaluate foraging decisions of females when faced with a series of nectar-aphid combinations.

## Materials and methods

### Insects and plants

Pea aphids were reared on fava bean plants in a growth chamber (16:8 L:D; 22.0 °C, 19.0 °C). *Coleomegilla maculata* colonies originated from individuals, field collected in Beltsville, MD, USA and were maintained in the lab at 28.0 °C at 18:6 L:D photoperiod (Lundgren et al. 2011). Thirty females were removed from colonies and placed in individual clear, plastic 1 oz. cups with a water wick and Lundgren's Super C. mac diet (Lundgren et al. 2011). Cups were monitored daily for the production of eggs, which were separated from their mothers within 24 h. Larvae were fed excess diet through eclosion. Upon eclosion, adult females were placed in a new cup and fed Super C. mac diet. Females were starved for 24 h prior to the start of the experiment.

Fava beans (*Vicia faba* L.) were grown in a soil mix (field soil, peat moss, and vermiculite in a 4:2:1 ratio) and were watered daily with approximately 60 ml of water per day. When the plants had 3–6 fully expanded leaves and extrafloral nectaries were visible, plants were removed from the soil and roots submerged in water. Individual plants were placed in a 50 ml plastic centrifuge tube filled with water. Parafilm (Pechiney Plastic Packaging, Menahsa, WI, USA 54952) was wrapped over the tube opening. The extrafloral nectaries were covered with Parafilm in the nectariless treatment. The other treatment had Parafilm wrapped around randomly selected stems and petioles, leaving the nectaries exposed. A single plant, with nectaries covered or exposed, was placed within one yellow, plastic Solo® cup. Another plastic Solo® cup, that had

the bottom removed, was placed mouth-to-mouth with the first and the two were sealed together with Parafilm. Cloth mesh was placed over the opening where the bottom of the top cup had been removed and secured with a rubberband. This created a cage in which the plant, aphids and female were contained. Each replication was placed within its own cage.

### Nectar availability and predation

There were seventeen replicates per treatment for a total of 34 experimental units. Fifty pea aphids were placed on plants within each cup. Week-old females were starved 24 h, then randomly assigned to either the treatment with nectaries covered or uncovered, along with a water-saturated cotton wick. Cups were checked daily. Each day the remaining aphids were removed, counted and replaced with 50 additional aphids. The assay continued for six days. On day six, lady beetles were removed from the assay and immediately frozen at −80 °C.

### Ovarian development

Females were thawed and their oocyte size was examined prior to quantifying nutrient reserves. The head, legs, and elytra of each individual were removed in saline solution (750 mg $NaCl_2$ [product #S271; Fisher Chemical Company, Fair Lawn, NJ], 350 mg KCl [product #P217, Fisher], and 280 mg $CaCl_2$ [product #349615000; Acros Organics, NJ, USA] in 1 l water). The ovaries were removed, and stained in Methylene blue solution (290 mg Methylene blue [product #414241000; Acros Organics] in 1 l water) for 2 min. The lengths and widths of the three largest oocytes in each ovary were measured using a micrometer (at 80×). The width was measured at the widest point of the oocyte. The volume of each oocyte was calculated as a cylinder (length × (0.5[width] × $\pi)^2$), and an average egg volume per female was calculated. The remainder of the body and any fat bodies in the saline solution were placed in a 1.5 ml microcentrifuge tube, and refrozen at −80 °C for nutrient analysis.

### Nutrient reserves

The amount of lipid and glycogen reserves found in each corpse was quantified using the colorimetric assays developed by van Handel (1985). Each corpse (and saline solution) was crushed into a 1.5 ml microcentrifuge tube containing 300 µl of methanol:chloroform (2:1) using a sterile plastic pestle. The mixture was then centrifuged at 13,200 rpm for 4 min, and the resulting supernatant and pellet were separated into glass test tubes. To quantify the lipid content of the beetle, 40 µl of sulfuric acid was added to the supernatant, and the solution was heated for 2 min at 90 °C. The tubes were cooled on ice, and 1950 µl of vanillin-phosphoric acid reagent (600 mg vanillin in 100 ml water, diluted in 400 ml of 85 % phosphoric acid; vanillin Product #V10-100; Fisher Chemical) was added to each tube. The solution was incubated at room temperature for 25 min, after which 200 µl was added to a 96-well plate. Optical density was recorded at 485 nm in a spectrophotometer (Hidex Plate Chameleon, Hidex, Finland). For a positive control, 200 µl of canola oil in 100 ml chloroform was added to six wells of the plate. No-lipid controls (200 µl vanillin reagent only) were added to six wells as a negative control. Next, the glycogen content of each beetle was determined using the pellet obtained previously. Specifically, 2,925 µl of anthrone reagent was added to each tube, and the resulting mixture was heated at 90 °C for 15 min. Following incubation, 200 µl of each sample was loaded onto a 96-well plate, and optical density was recorded at 590 nm using a spectrophotometer (Hidex Plate Chameleon, Hidex, Finland). For a positive control, 200 µl of glycogen solution (25 mg glycogen [from oyster, type II; Sigma] in 25 ml water) was added to six wells of the plate. No-lipid controls (200 µl anthrone reagent only) were added to six wells as a negative control.

### Attraction of nectaries

A Y-tube olfactometer assay was conducted to evaluate the response of *C. maculata* females to extrafloral nectar volatiles from *V. faba* and the influence of aphids on this response. Air was pumped from a laboratory bench nozzle through a flowmeter at the rate of 2.0 l $min^{-1}$ (Key Instruments, Trevose, PA, USA) (Bahlai et al. 2008). Air was then pushed over activated charcoal through Teflon tubing (0.6 cm od). PVC pipes (35.5 × 10 × 11.2 cm, h × id × od) sealed with glass plates (12 cm diameter) on each end served as the odor source containers. Air passed over the odor source and into the glass Y-tube (Analytical Research

Systems, Gainesville, FL, USA). A flow meter was also placed on the third arm of the Y-tube to ensure that the flow remained constant. At the beginning of each day of experiments, the system was checked to ensure equal flow of air through each arm.

Plant material used to establish nectar attraction was *V. faba* plants grown in the greenhouse. Plants were grown in the greenhouse until they reached the 3–6 node stage. At this stage plants were removed from the soil and placed into 50 ml tubes of water, as described above. The extrafloral nectaries (EFN) were covered with Parafilm in the nectariless treatment. The other treatment had Parafilm wrapped around randomly selected stems and petioles, leaving the nectaries exposed. Two additional treatments included plants with nectaries covered and plants with nectaries exposed, each with 25 pea aphids. Aphids were placed on plants at least 2 h prior to the start of the experiments to ensure they had established and began feeding. The experimental design was factorial, so that all treatments were contrasted for a total of six comparisons. Comparisons were randomly selected during each day of experiments. The arm of the Y-tube at which the odor source was placed was randomly determined, so as to ensure no bias. One month old *C. maculata* females from the laboratory colony were starved 18–24 h prior to the start of experiments. Females were introduced into the Y-tube and given 10 min to make a choice. A choice was determined when an individual traveled 4 cm past the intersection of the olfactometer arms and remained there for 15 s. Females that did not make a choice in 10 min. were excluded from the analysis. The Y-tube and odor containers were rinsed with ethanol and distilled water, then dried after every trial. New plant material and females were used in each trial. The tube was rotated after every ten trials to ensure there was no bias toward one side.

### Data analysis

A repeated-measures ANOVA was conducted to determine variation in aphid consumption (number consumed) over time between treatments. Treatment was the between-subject effect, and time and time × treatment were within-subject effects. The number of aphids consumed over time was graphed and single exponential decay curves fitted to the data. The effect of treatment on female oocyte volume was analyzed using a repeated-measures ANOVA. The volume of each individual oocyte was calculated and those volumes were the dependent variables in this analysis. Treatment and replicate (17 individuals per treatment) were between-subject effects and oocyte volume (six largest oocytes per female were measured), oocyte volume by replicate and oocyte volume by treatment were within-subject effects. Absorbances recorded for lipid and glycogen analysis were compared between treatments using a *t* test. Mean oocyte size per female was correlated with glycogen and lipid absorbances by linear regression analysis. For the olfactometer assay, preference between each treatment comparison was determined by a contingency table analysis. Additionally, in an effort to evaluate the overall relationship between aphids and extrafloral nectaries, a $2 \times 2$ contingency table was developed and analyzed with the null hypothesis that aphid presence or absence will not affect how *C. maculata* females respond to extrafloral nectaries. The table was constructed with extrafloral nectar presence or absence in the columns and aphid presence or absence in rows. For each trial, the nectar, aphid combination that was selected by the female was given a one. These numbers were summed and the total number of times that each combination was selected comprised the contingency table. The percentage of each treatment combination that was selected throughout the study was calculated with a null expected percentage of 25 % for each. The Yate's $\chi^2$ is reported and corrected for continuity. All statistics were conducted using Systat 11 (Systat Software Inc., Chicago, IL, USA).

## Results

### Sugar availability and predation

The number of aphids consumed daily was significantly greater among *C. maculata* females that had no access to plant extrafloral nectaries ($F_{1,32} = 4.54$; $P = 0.04$) (Fig. 1). The mean (±SE) number of aphids consumed daily in treatments with exposed nectaries was 35.2 (±1.11), and with covered nectaries 38.5 (±1.00) for the duration of the experiment. Number of aphids consumed decreased significantly over time regardless of treatment ($F_{5,160} = 33.67$; $P < 0.0001$) (Fig. 1). The interaction effect between treatment and day was not statistically significant ($F_{5,160} = 57.64$; $P = 0.39$). There was no significant

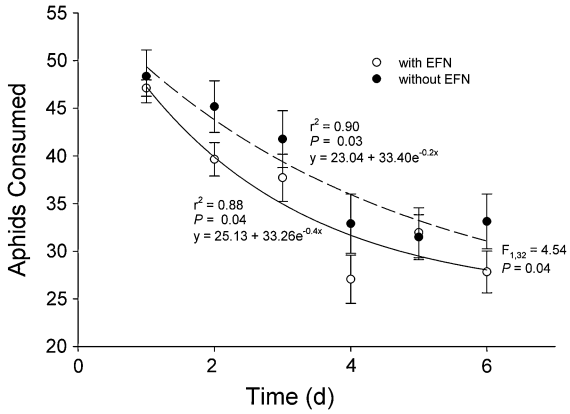


**Fig. 1** Aphid consumption over time by *C. maculata* either provided extrafloral nectar (EFN) or not. Relationships between the mean (±SE) number of aphids consumed daily over time are presented as exponential decay curves for each treatment ($\alpha = 0.05$)

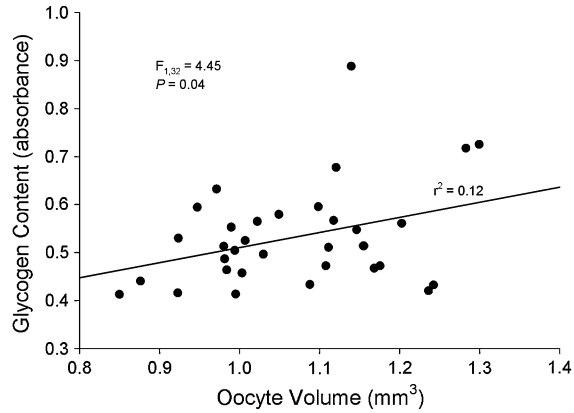


**Fig. 2** Correlation between glycogen content and oocyte volume of *C. maculata* females. A single point represents one individual. Oocyte volume is an average of the six largest oocytes measured for each individual. Glycogen content was assessed by conducting the hot anthrone assay and determining absorbance

difference between the mass of aphids fed to each treatment ($F_{1,100} = 0.04$; $P = 0.85$).

## Ovarian development

Mean oocyte volume was greater in females with access to prey (1.11 ± 0.02) than in females fed both prey and nectar (1.03 ± 0.02); however, this difference was not statistically significant ($F_{1,31} = 3.60$, $P = 0.07$). Oocyte volume did not vary significantly by replicate ($F_{1,31} = 0.39$, $P = 0.54$). The within subject factor of oocyte volume did not vary significantly ($F_{5,155} = 0.27$, $P = 0.93$), nor did the volume by treatment ($F_{5,155} = 0.54$, $P = 0.75$) or volume × replicate interactions ($F_{5,155} = 1.01$, $P = 0.42$).

## Nutrient reserves

Glycogen and lipid absorbances were similar in both treatments ($t_{32} = 0.30$; $P = 0.77$ and $t_{32} = 0.46$; $P = 0.65$, respectively). Glycogen content of females (pooled across treatments) was significantly correlated with mean oocyte volume at the time of dissection ($F_{1,32} = 4.45$; $P = 0.04$) (Fig. 2). Lipid content of females was not correlated with oocyte volume ($F_{1,32} = 0.64$; $P = 0.43$).

## Attraction of nectaries

The majority of females placed in the Y-tube olfactometer made a choice with percentages varying from 83 to 93 %, depending on treatment. Female *C. maculata* chose *V. faba* plants with nectaries covered significantly fewer times than when offered plants with nectaries exposed (Table 1). In the absence of nectaries, females responded to green leaf volatiles, selecting plants with aphids significantly more often than plants without. There was no significant difference in treatments when females were given the choice between nectaries or aphids with an almost equal percentage of individuals selecting each treatment. When the treatment of exposed extrafloral nectaries with aphids was part of the assay, in all three comparisons (EFN+, aphid+ versus EFN+, aphid−; EFN−, aphid−; EFN−, aphid+), the preference could not be distinguished (Table 1). The contingency table analysis demonstrated the overall patterns of selection by female *C. maculata*. Treatments with only nectaries or aphids were selected in greatest proportion, 33 % and 27 % of the time, respectively. Treatments with both exposed extrafloral nectaries and aphids were chosen 25 % of the time, while treatments with neither aphids, nor nectaries were chosen only 16 % of the time. The contingency table analysis indicated that the presence or absence of aphids influences how *C. maculata* females respond to extrafloral nectaries ($\chi^2 = 5.87$, df = 1, $P = 0.015$), thus corroborating results when individual trials were analyzed.

**Table 1** Preference of *C. maculata* females to the volatiles produced by aphids and extrafloral nectar (EFN). EFNs from *V. faba* and pea aphids (*Acyrthosiphon pisum*) were the focal foods, and choice studies were conducted in a Y-tube

| Odor source comparison | | *N* | (%) Response | (%) Choice | | $\chi^{2a}$ | *P* |
|---|---|---|---|---|---|---|---|
| 1 | 2 | | | 1 | 2 | | |
| EFN+, aphid− | EFN−, aphid− | 30 | 93 | 79 | 21 | 9.14 | 0.002 |
| EFN−, aphid− | EFN−, aphid+ | 34 | 85 | 31 | 69 | 4.17 | 0.041 |
| EFN+, aphid− | EFN−, aphid+ | 30 | 83 | 48 | 52 | 0.04 | 0.841 |
| EFN+, aphid− | EFN+, aphid+ | 47 | 85 | 58 | 43 | 0.90 | 0.343 |
| EFN−, aphid− | EFN+, aphid+ | 30 | 87 | 50 | 50 | 0.00 | 1.000 |
| EFN+, aphid+ | EFN−, aphid+ | 30 | 90 | 48 | 52 | 0.04 | 0.847 |

[a] 1 df for all contrasts

## Discussion

The availability of extrafloral nectaries influences the number of prey items consumed. However, the benefit of a mixed diet was not immediately obvious through measurements of oocyte size or nutrient reserves. Olfactometer studies demonstrated that extrafloral nectaries are attractive to this predator. In a closed system with a single predator, nectar availability reduced predation rates. However, in natural settings it is possible that the attractiveness of the extrafloral nectaries could increase predator abundance to such an extent that a slight decline in per capita predation will not have deleterious effects on predation intensity (Lundgren 2009a).

*Coleomegilla maculata* females consumed fewer aphids when aphids were offered in conjunction with nectaries, suggesting both food sources are being consumed in spite of aphids' presumed superior nutritional contents. Similar results have been observed in *Coccinella transversoguttata* Faldermann and *Harmonia axyridis* (Pallas) which consumed fewer prey when also provided sugar water and extrafloral nectaries respectively (Richards and Evans 1998; Spellman et al. 2006). Nutritional analysis and measurements of the ovaries demonstrate that nectar provides no obvious benefit relative to or in conjunction with prey. However, when no other food is available (e.g., during springtime) extrafloral nectar increases survival, fecundity and nutrient reserves (Lundgren and Seagraves 2011). The positive association between glycogen content and oocyte size has been observed previously (Lundgren and Seagraves 2011). The presented data suggests that consumption of both aphid prey only and a mixed diet of aphid prey and nectar allows *C. maculata* to maintain glycogen nutrient reserves and have similar reproductive capabilities. A meta-analysis demonstrated that coccinellid adult performance and reproduction are improved when females are offered a mixed diet of sugar and prey (Lundgren 2009b). It is possible that egg production in the mixed diet treatment of the current experiment may have been increased, but we did not evaluate this fitness parameter. During times of low nutrient availability, the predictability of plant provided nectar resources may offer an immediate and easily obtained source of carbohydrates and energy. Wäckers (1994) demonstrated that parasitoid wasps show a preference for flower odors when starved. However, if parasitoids had consumed a sugar meal, odors from prey-damaged plant material were preferred.

Olfactometer studies determined that the extrafloral nectaries of *V. faba* and pea aphids are attractive to *C. maculata* when offered independently. Volatile attractants of EFN to predators have been suggested previously, but the empirical evidence has been lacking. Stapel et al. (1997) report that *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) females located extrafloral nectaries on cotton more quickly than areas where sucrose or sucrose with vanilla was applied, suggesting that volatile production by nectaries is attracting parasitoids. The attractive components of extrafloral nectar consist of sugars and amino acids (Van Emden and Hagen 1976; González-Teuber and Heil 2009a, b; Pacini and Nicolson 2010). Baker et al. (1978) identified 15 amino acid components in the extrafloral nectar of *V. faba*, which may be one nectar constituent that helps to attract insect species to the nectar source (Hagen

et al. 1976; Lanza 1988) and encourage pollination (González-Teuber and Heil 2009b). Additional work on the attractive chemistry of extrafloral nectars would help to inform how this aspect of the plant defense system functions against herbivores and potentially distracts predatory insects from their prey. Previous research has demonstrated that predators are attracted to aphid-produced volatiles, such as honeydew and alarm pheromones, as well as green leaf volatiles resulting from aphid damage (Hatano et al. 2008), supporting the observation that females select plants with feeding aphids when no nectaries are present. Positive antennal responses of *C. maculata* adults to green leaf volatiles and both sex and alarm pheromones of pea aphids have been documented (Zhu et al. 1999). *Coleomegilla maculata* foraging decisions may be solely dictated by the physiological requirements of the female or perhaps EFN-produced volatiles play some role in distracting females from their aphid prey.

Simultaneous availability of aphids and extrafloral nectaries unexpectedly disrupted the clear preferences displayed by *C. maculata* for these foods when they were offered individually. It was assumed that the combination of two attractive food sources would lead to an obvious choice. This was not the case in our experiment. We hypothesize that aphids are affecting the production of volatiles by the host plant. Sakata and Hashimoto (2000) observed that non-myrmecophilous aphids repel ants from plants with extrafloral nectaries, in an effort to avoid predation. Schwartzberg et al. (2011) trapped volatiles as they were emitted by *V. faba* being fed upon by pea aphids. They observed variations in volatiles emitted from control plants with and without aphids: all but one of the 11 major compounds emitted were diminished by aphid herbivory. Volatiles produced from caterpillar (Lepidoptera: Noctuidae) feeding were suppressed when both aphids and caterpillars were present on the plant (Schwartzberg et al. 2011). This work supports the idea that *V. faba* plants with exposed nectaries that are fed upon by pea aphids are not attractive to predators, and aphids may in fact be altering the emission of volatiles to decrease plant attraction. Future work identifying the volatiles associated with extrafloral nectar attraction, comparing volatiles of plants with exposed and covered nectaries, will indicate which compounds are being produced specifically by nectaries.

Despite decreased per capita consumption when sugar resources are present in a closed system, it is possible that the increase in predator numbers that result from the incorporation of sugar and other non-prey resources into a landscape could reduce prey numbers (Eubanks and Denno 1999, 2000; Lundgren 2009a). Additionally, when prey are not available or abundant, the consumption of non-prey foods such as sugar increases predator survival (Lundgren and Seagraves 2011) and prevents movement from areas where control may be needed later in the season (Landis et al. 2000). Incorporation of sugar in the form of extrafloral nectaries may or may not prove useful in increasing numbers of natural enemies and decreasing pest insects. Field studies are necessary to fully understand how attraction to nectaries will affect predation rates on target pest insects. Identification of volatiles produced by nectaries and the influence of aphids on that production will provide even greater insight into efforts to enhance natural enemy diversity throughout agricultural cropping systems.

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## Author Biographies

**Beth A. Choate** The research described in this work is part of a post-doctoral research project of Beth Choate while working with the USDA-ARS. Methods of increasing insect natural enemy abundance and manipulating behaviors to increase predation rates were the objectives of her research program.

**Jonathan G. Lundgren** is an insect ecologist with USDA-ARS, USA who studies beneficial insect conservation, predator ecology, the ecological risk posed by new pest management technologies, and the design of sustainable crop production systems that minimize pesticide inputs. Increasing biodiversity and reducing disturbance to agroecosystems are key themes of his program.