

## Laboratory and Field Evaluation of Host-Related Foraging Odor-Cue Combinations to Attract *Drosophila suzukii* (Diptera: Drosophilidae)

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### Abstract

The invasive spotted-wing drosophila, *Drosophila suzukii* (Matsumura), is a major pest of soft-skinned fruits. Since its introduction into North America and Europe, significant progress has been made in understanding the volatile cues used by this fly during food, oviposition site, and mate finding. Despite this progress, commercially available lures are non-selective. Here, we tested two *Hanseniaspora uvarum* (Niehaus) yeast compounds (isoamyl acetate and isobutyl acetate) and a leaf compound  $\beta$ -cyclocitral alone and in combination with a blend of four fermentation compounds ('Fermentation lure': acetic acid, ethanol, methionol, and acetoin) to improve *D. suzukii* attraction and selectivity. In laboratory assays, males and females were attracted to all seven individual compounds, although in electrophysiological assays, their antennae exhibited a dose-dependent response to only four of these compounds. In two-choice cage studies, the Fermentation lure was more attractive to *D. suzukii* than water controls, whereas  $\beta$ -cyclocitral and the mixture of isoamyl acetate and isobutyl acetate were not attractive in this larger-cage study. Moreover, adding the two-component *H. uvarum* compound blend to the Fermentation lure reduced *D. suzukii* attraction to the Fermentation blend. When these experiments were repeated in blueberry, raspberry, blackberry, and cherry orchards across several states in the United States over 2 yr, similar outcomes were observed:  $\beta$ -cyclocitral or the mixture of the *H. uvarum* blend did not improve the attractiveness of the Fermentation lure or its selectivity. This study demonstrates that cues from different sources may interfere with each other and reduce *D. suzukii* attraction to otherwise attractive odor combinations.

**Key words:** spotted-wing drosophila, invasive pest, attractant, yeast, behavior-based strategy

In some insects, the combinations of volatile compounds from different sources can be used synergistically to increase their attraction. The most pronounced synergistic attraction occurs between host-plant odor compounds and insect pheromones (Reddy and Guerrero 2004). The majority of these interactions have been described in Lepidoptera and Coleoptera, and Xu and Turlings (2018) provide an overview of the described cases across five insect orders. For example, host-plant odors synergize with major sex pheromone components of the corn earworm [*Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae)] (Light et al. 1993), the European grapevine moth [*Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae)] (von Arx et al. 2012), and the codling moth [*Cydia pomonella* (L.) (Lepidoptera: Tortricidae)] (Light et al. 1993, Yang et al. 2004) to increase moth attraction compared to either odor source alone. Similar scenarios have been described in Coleoptera (Dickens 1989, Lin et al. 1992). Fewer cases of odor synergisms have been observed in Diptera, although the mechanism of one specific host odor-pheromone synergism was recently described in the generalist species and model organism *Drosophila melanogaster* (Meigen) (Diptera: Drosophilidae) (Das et al. 2017).

Like most frugivorous insects, vinegar flies (*Drosophila* spp.) use a variety of volatile cues for host location. One such fly is the spotted-wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), an invasive pest from Southeast Asia (Walsh et al. 2011, Asplen et al. 2015) and a major pest of fruit crops, including stone fruits, blueberry, strawberry, raspberry, and blackberry (Beers et al. 2011, Hauser 2011). Unlike other *Drosophila* flies in the melanogaster group, which prefer rotten fruit for oviposition and larval development, *D. suzukii* females pierce the flesh of ripening and ripe fruit with their serrated ovipositor (Karageorgi et al. 2017). Due to their high fecundity and preference for fresh fruit, *D. suzukii* has become an important invasive insect pest in North and South America (Lee et al. 2011, Deprá et al. 2014) and Europe (Calabria et al. 2012, Cini et al. 2012). Large and mobile populations make this insect difficult to manage (Klick et al. 2016).

Similar to other vinegar flies in the melanogaster group, *D. suzukii* flies appear to also use volatiles from fermentation products to locate food (Landolt et al. 2012, Karageorgi et al. 2017, Cloonan et al. 2018) and potentially also mating sites (Cloonan et al. 2018). Attractive fermentation volatiles have been identified and exploited for the development of monitoring lures (Cha et al. 2012, 2013, 2014, 2015, 2017, 2018; Landolt et al. 2012; Kleiber et al. 2014; Adams et al. 2017; Akasaka et al. 2017). In addition to fermentation odors used in food-source location, *D. suzukii* flies are also attracted to yeast (Hamby et al. 2012, Scheidler et al. 2015), leaf (Keesey et al. 2015), and fruit odors (Abraham et al. 2015, Dekker et al. 2015, Revadi et al. 2015a, Cloonan et al. 2018), although the behavioral significance of these odors have not been fully investigated.

Current commercially available monitoring lures are not selective and can have significant by-catch numbers (Cha et al. 2013, Burrack et al. 2015, Alnajjar et al. 2017, Jaffe et al. 2018). Sorting through these by-catches, typically non-*D. suzukii* drosophilids, is time-intensive, costly, and often not feasible for fruit growers without entomology expertise. A more attractive and selective *D. suzukii* lure could increase trap specificity and usability for fruit growers. It may be that odors from previously identified sources synergize in combination to increase *D. suzukii* attraction. Food-seeking *D. suzukii* may cue in on yeast, leaf, or fruit odors in combination with fermentation odors when searching for suitable feeding sites. For example, Jaffe et al. (2018) found that the addition of a yeast (*Saccharomyces cerevisiae* (Meyen ex. E.C. Hansen)) and sugar bait to a commercially available fermentation-based lure (Scentry Biologicals Inc.,

Billings, MO) additively increased *D. suzukii* attraction in blueberry and raspberry fields. However, *Hanseniaspora uvarum* (Niehaus), and not *S. cerevisiae*, is the most prevalent and attractive yeast isolated from *D. suzukii*, in particular two antennally-active volatiles, isobutyl acetate and isoamyl acetate, have been identified from *H. uvarum* (Hamby et al. 2012, Scheidler et al. 2015). Moreover, Keesey et al. (2015) identified  $\beta$ -cyclocitral, a leaf volatile from strawberry, to be more attractive to *D. suzukii* than to other drosophilids. Addition of these *H. uvarum* and leaf volatiles could thus help increase the attractiveness and specificity of existing *D. suzukii* lures.

Therefore, the goal of this multistate study was to investigate if combinations of different compounds could increase the attraction and selectivity of *D. suzukii* adults across multiple crops. Because fermentation, yeast, and leaf compounds are cues from the host-plant habitat that may be used by *D. suzukii* flies during food location (Revadi et al. 2015a, Cloonan et al. 2018), we hypothesized that adding *H. uvarum*- (isobutyl acetate and isoamyl acetate) and leaf- ( $\beta$ -cyclocitral) associated compounds increases fly attraction and selectivity to an attractive fermentation-based lure. To this end, we first examined in the laboratory the antennal and behavioral responses of adult *D. suzukii* to previously identified compounds from fermentation, yeast, and leaf odor sources via electroantennography (EAG) and choice assays. We next examined the attractiveness of these compounds singly and as lure combinations, in the laboratory as well as in the field across several U.S. states and in different fruit types.

## Materials and Methods

### Insects

*Drosophila suzukii* flies (males and females) were reared using protocols previously described (Rodriguez-Saona et al. 2019). Briefly, flies were obtained in 2013 from a field-captured population in Atlantic County, NJ and maintained at the Rutgers P.E. Marucci Center, Chatsworth, NJ. These flies were maintained on an artificial drosophila diet modified from Jaramillo et al. (2015). Fly colonies were kept in an incubator (Percival Scientific, Perry, IA) at 25°C, 55% relative humidity, and a 16:8 light:dark (L:D) cycle (Jaramillo et al. 2015). Sexually mature and mated flies, 3–5 d old (Revadi et al. 2015b), were used for the electrophysiology and laboratory behavioral assays.

### Odor Compounds

We tested seven volatile compounds, alone and in various combinations, for their attractiveness to *D. suzukii*, which included four fermentation-based compounds: 1) ethanol, 2) acetic acid, 3) acetoin, and 4) methionol (Cha et al. 2014) (hereon referred to as ‘Fermentation lure’); two *H. uvarum* yeast-derived compounds: 5) isobutyl acetate and 6) isoamyl acetate (Hamby et al. 2012, Scheidler et al. 2015) (hereon referred to as ‘*H. uvarum* lure’), that induce higher olfactory responses from *D. suzukii* than *D. melanogaster* (Scheidler et al. 2015); and a strawberry leaf-derived terpenoid: 7)  $\beta$ -cyclocitral (Keesey et al. 2015) (hereon referred to as ‘Leaf lure’). All compounds had  $\geq 98\%$  purity and were purchased from Sigma-Aldrich (St. Louis, MO).

### EAG Assays

Studies were conducted to compare the antennal response of adult male and female *D. suzukii* to volatiles described above. The antennal responses of male and female *D. suzukii* to each individual compound were tested at five different doses (1 mg, 100  $\mu$ g, 10  $\mu$ g, 1  $\mu$ g, and 100 ng) diluted in hexane. The stimulus cartridge preparations, antennal preparations, and EAG apparatus used were

similar to those described in Williams et al. (2008). Briefly, stimulus applicators consisted of a 14.5-cm-long glass Pasteur pipette containing 10  $\mu$ l of a test compound- or hexane-(control)-impregnated onto a 6  $\times$  0.5-cm strip of filter paper (Whatman No. 1; Whatman International Ltd., Maidstone, Kent, UK) (Williams et al. 2008). Impregnated filter paper pieces were placed under the fume hood for 2 min to allow the hexane to evaporate. The recording and base electrodes used for the EAG recordings consisted of drawn capillary tubes filled with phosphate-buffered saline (NaCl, 4 g;  $\text{Na}_2\text{HPO}_4$ , 0.57 g;  $\text{KH}_2\text{PO}_4$ , 0.1 g; KCL, 0.1 g in 500 ml distilled water). A silver wire was inserted into these saline-filled capillary tubes. The base electrode was fixed to the thorax of the adult fly by excising the abdomen and piercing the sharp tip of the pulled capillary directly into the thoracic cavity. Once the fly preparation was mounted, the recording electrode was carefully moved toward the antenna using a micromanipulator until one of the antennae touched the pool of saline solution on the recording electrode. Antennal preparations were exposed to a constant stream of charcoal-filtered and humidified air at a rate of 1.5 l/min.

The EAG apparatus consisted of an IDAC-02 interface board for data acquisition and used Syntech software (Syntech Ltd., Hilversum, The Netherlands) for recording, storing, and quantifying EAG responses. Antennal preparations were exposed to each of the seven test compounds at each of the five concentrations and a hexane control in a random order. Preparations were exposed to one stimuli (compound/concentration) at a time and then removed and discarded once eight random stimuli (7 compounds plus an hexane control) were presented to an antennal preparation; five antennae were tested per day, so that the entire 36 (7 compounds  $\times$  5 concentrations plus hexane control)-stimuli panel was tested in one particular day. Test and control compounds were applied at 30-s intervals at a pulse rate of 0.5 s, with a 2-min interval in between each stimulus. Maximum amplitudes of depolarizations were measured for each of the 36-stimuli panel tested, and each panel was tested on 15 different individuals of each sex.

## Laboratory Behavioral Assays

### Individual Compounds

First, we analyzed the attraction of *D. suzukii* adults to single volatile compounds from the Fermentation, *H. wuvarum*, and Leaf lures compared to water controls. The assays used plastic deli containers (946 ml, 11.5 cm diameter, 14.3 cm high) (Supp Fig. S1 [online only]) as release arenas partitioned with moistened pieces of cotton for adult flies to consume ad libitum, as described in Feng et al. (2018). The lid of each arena had an 80-mm diameter circular hole covered with a nylon mesh to provide ventilation. Each arena contained two clean drosophila rearing flasks (177 ml, 1.7 cm diameter, 6.5 cm high) as trap containers. Test compounds were applied to a small piece of dental cotton impregnated with either 20  $\mu$ l of an individual test compound (neat) or 20  $\mu$ l of water as a control inside of a 1.5-ml Eppendorf tube (Feng et al. 2018). These Eppendorf tubes were then placed at the bottom of the drosophila rearing flask trap container. A small piece of parafilm was used to cover the openings of each of these rearing flask trap containers and a small hole, ca. 3 mm in diameter, was punctured in the center to allow adult *D. suzukii* to fly inside. Flies that entered these flasks were unable to escape (K.C., personal observations), and we could thus record the attraction of adult flies to individual compounds compared to water controls. Five different arenas, each containing five male and five female flies, were replicated for each individual compound versus water control combination (i.e., total of  $n = 50$  flies tested per compound). These arenas were left inside a fume hood in the laboratory (25°C) under

artificial light (15:9 L:D cycle) for 48 h. Those flies that did not make a decision during these 48 h were treated as 'nonresponders' (Feng et al. 2018).

### Single Lures

Next, we examined the attractive behavior of *D. suzukii* adults to combinations of compounds (lures) compared to a water control. The 'Fermentation lure' was prepared comprising of 1 ml 1:2 ratio of methionol:acetoin in an Eppendorf tube and acetic acid plus ethanol mixed in a drowning solution at 1.6 and 7.2%, respectively (Cha et al. 2014); a two-component '*H. wuvarum* lure' was prepared comprising of isobutyl acetate and isoamyl acetate at a 1:1 ratio, a ratio based on emissions from *H. wuvarum* (Scheidler et al. 2015); and a single-component 'Leaf lure' was prepared comprising of only  $\beta$ -cyclocitral (Table 1). The compounds were passively released in these assays through open Eppendorf tubes. For this set of laboratory experiments, we used 30-cm<sup>3</sup> mesh cages (BioQuip Products, Rancho Dominguez, CA) as release arenas. Each release arena contained two clear deli containers (946 ml, 11.5 cm diameter, 14.3 cm high) with mesh lids as trap containers. Each deli container had 15 holes (ca. 3 mm in diameter) punched around the top of the container 2 cm below the lid for flies to enter. Inside each deli container, a small, yellow sticky card (5 cm<sup>2</sup>) was hung from the lid that acted as a trap for flies entering the deli cups and was suspended over a drowning solution (300 ml of tap water plus one drop of soap) (Supp Fig. S2 [online only]). A 1.5-ml Eppendorf tube containing a cotton ball impregnated with 1 ml of an individual lure type (according to Feng et al. 2018) was also hung from the lid inside of each container. Choice tests consisted of: 1) a bait based on a commercial yeast (*S. cerevisiae*; Red Star Active Dry Yeast, Lesaffre Yeast Corporation, Milwaukee, WI) plus sugar (as a positive control; Burrack et al. 2015, Jaffe et al. 2018) versus blank (water); 2) Fermentation lure (as described above) versus blank (water); 3) 1 ml *H. wuvarum* lure versus blank (water); and 4) 1 ml Leaf lure versus blank (water). Fifteen male and 15 female flies were released into each 30-cm<sup>3</sup> mesh cage and left for 24 h on a laboratory bench (25°C, 15:9 L:D cycle) in near natural sunlight. Each combination of lure versus no lure (blank) control was replicated four times (i.e. total of  $n = 120$  flies tested per treatment). After 24 h, the numbers of flies inside the deli container drowning solution and stuck to the yellow sticky cards were counted, and all containers and materials were discarded.

### Combined Lures

The Fermentation lure was the most attractive lure to *D. suzukii* flies from the 'Single Lures' cage experiment described above (see Results). Thus, we next wanted to examine whether the addition of isoamyl acetate and isobutyl acetate (*H. wuvarum* lure), and  $\beta$ -cyclocitral (Leaf lure) increases the attraction of *D. suzukii* flies to the Fermentation lure. For this, in the last set of laboratory behavioral experiments, we replicated the design of the previous behavioral assays using the 30-cm<sup>3</sup> mesh cage release arenas and two deli containers (946 ml, 11.5 cm diameter, 14.3 cm high) as traps. Choice tests consisted of the Fermentation lure (prepared as described above) versus the Fermentation lure plus a separate Eppendorf tube containing either 1) 1 ml Leaf lure, 2) 1 ml *H. wuvarum* lure, 3) 500  $\mu$ l Leaf lure and 500  $\mu$ l *H. wuvarum* lure, 4) 500  $\mu$ l *H. wuvarum* lure, 5) 100  $\mu$ l *H. wuvarum* lure, 6) 500  $\mu$ l isoamyl acetate, or 7) 500  $\mu$ l isobutyl acetate. Again, 15 female and 15 male *D. suzukii* flies were added to each release arena and left on the laboratory bench exposed to natural sunlight for 24 h, after which adult flies inside the deli container drowning solution and stuck to the yellow sticky cards were counted, and all materials were subsequently discarded. Each

**Table 1.** Lure and bait treatments tested for trapping *Drosophila suzukii* in the laboratory and in the field (2016–2017 and 2017–2018 seasons)

Treatment/Lure name	Components (per trap)	Components (per lure)
Fermentation	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin
Leaf	500 ml of water + one drop of liquid soap	β-cyclocitral 1 ml
<i>H. uvarum</i>	500 ml of water + one drop of liquid soap	500 µl of isobutyl acetate + 500 µl of isoamyl acetate
Fermentation + <i>H. uvarum</i> (1 ml)	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin + 500 µl of isobutyl acetate + 500 µl of isoamyl acetate
Fermentation + <i>H. uvarum</i> (500 µl)	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin + 250 µl of isobutyl acetate + 250 µl of isoamyl acetate
Fermentation + <i>H. uvarum</i> (100 µl)	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin + 50 µl of isobutyl acetate + 50 µl of isoamyl acetate
Fermentation + Leaf (1 ml)	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin + β-cyclocitral 1 ml
Fermentation + <i>H. uvarum</i> (1 ml) + Leaf (1 ml)	456 ml of water + 8 ml acetic acid + 36 ml ethanol + one drop of liquid soap	333 µl of methionol + 666 µl of acetoin + 500 µl of isobutyl acetate + 500 µl of isoamyl acetate + β-cyclocitral 1 ml
Yeast and sugar	5.07 g of dry active yeast + 25.35 g of sugar in 450 ml of water + one drop of liquid soap	Nothing (only the tube)
Control	500 ml of water + one drop of liquid soap	Nothing (only the tube)

lure combination was replicated six times (i.e., total of  $n = 180$  flies tested per treatment).

### Field Behavioral Assays

A 2-yr study was conducted across multiple regions and crops to test the response of *D. suzukii* to individual (2016) and combinations (2017) of the Fermentation, *H. uvarum*, and Leaf lures (used in laboratory assays) under field conditions. In all field assays, trapping was performed in fields with ripe fruit (i.e., during harvest). In addition, in New Jersey blueberries, traps were maintained in fields before and after the harvest period to test the response of flies to lures in the absence of fruit. Lures were placed and serviced according to the dates in [Supp Table S1](#) [online only]. In 2016, we compared *D. suzukii* capture in traps containing individual lures (i.e., Fermentation, *H. uvarum*, and Leaf lures) along with a blank (no lure) control (as a negative control) and a bait based on a commercial yeast (*S. cerevisiae*) plus sugar (as a positive control). Lures were formulated as described in [Table 1](#), 1 ml of each lure was loaded into an 1.5-ml Eppendorf tube containing a cotton ball, deployed in Yellow Jacket and Flying Insect Traps (product number M362; Victor Pest Control Solutions, Lititz, PA), and suspended over a drowning solution (500 ml water + 0.24 ml unscented soap) (methods followed those described in [Feng et al. 2018](#)). Individual lures were compared at nine locations across six U.S. states in highbush blueberry, lowbush blueberry, tart cherry, blackberries, and raspberries. In 2017, we compared four lure combinations: 1) Fermentation lure alone, 2) Fermentation lure plus *H. uvarum* lure, 3) Fermentation lure plus Leaf lure, and 4) Fermentation lure plus *H. uvarum* and Leaf lures. Each lure type was prepared in separate Eppendorf tubes. In addition, we included a water control and yeast plus sugar bait ([Table 1](#)). These six treatments were compared at seven locations across six U.S. states in highbush blueberry, lowbush blueberry, tart cherry, blackberries, and raspberries.

Within each location, each treatment was replicated between two to five times as a randomized complete block design and blocks were spaced at least 15 m apart. Individual traps within each block were spaced at least 3 m apart. Traps in all states were

deployed before fruit ripening, at the top of the crop canopy, for 4–8 wk until the end of harvest depending on the phenology of the fruit crop. In each week, the contents of the drowning solution were collected and replaced with clean drowning solution. Lures were also replaced bi-weekly (i.e., every 14 d) for each lure type, and the location of each trap was rotated to control for potential positional effects. In New Jersey, in addition to assessing captures of *D. suzukii* to lures during the growing season, traps were continually serviced for the entire 2016–2017 and 2017–2018 year to compare the attractiveness of the lures during the cropping season and during the off-season.

To determine female reproductive status, a subsample of 1–10 randomly selected female *D. suzukii* from each lure type at each location, depending on availability, was sent to the Rutgers P.E. Marucci Center, Chatsworth, NJ for dissections. Dissections and assessment of female reproductive status were performed according to the methods described in [Avanesyan et al. \(2017\)](#) and [Grassi et al. \(2018\)](#). Samples were preserved in 70% ethanol and dissected under a stereomicroscope. The total number of mature eggs was counted for each sample.

### Statistical Analyses

Nonparametric tests were used to analyze EAG and field data because they were not normally distributed. Total antennal depolarizations for each compound at each concentration between male and female *D. suzukii* were analyzed with a Kruskal–Wallis test followed by nonparametric multiple comparisons for each pair using the Wilcoxon method. The attraction of adult flies to different combinations of individual compounds and lures in the laboratory behavioral assays was analyzed using *t*-tests.

For both the 2016 and 2017 in-field seasons across all states and fruit types and in-season versus off-season comparison in New Jersey, analyses of absolute *D. suzukii* numbers, trap selectivity, and number of mature eggs per female per week were conducted with a Kruskal–Wallis test followed by nonparametric comparisons for each pair using the Wilcoxon method. A generalized linear model with a Poisson distribution was used to analyze the effects of season,

treatment, and treatment × season on the number of mature eggs per female during the in- and off-growing seasons for both years (2016–2017 and 2017–2018) in highbush blueberry in New Jersey.

**Results**

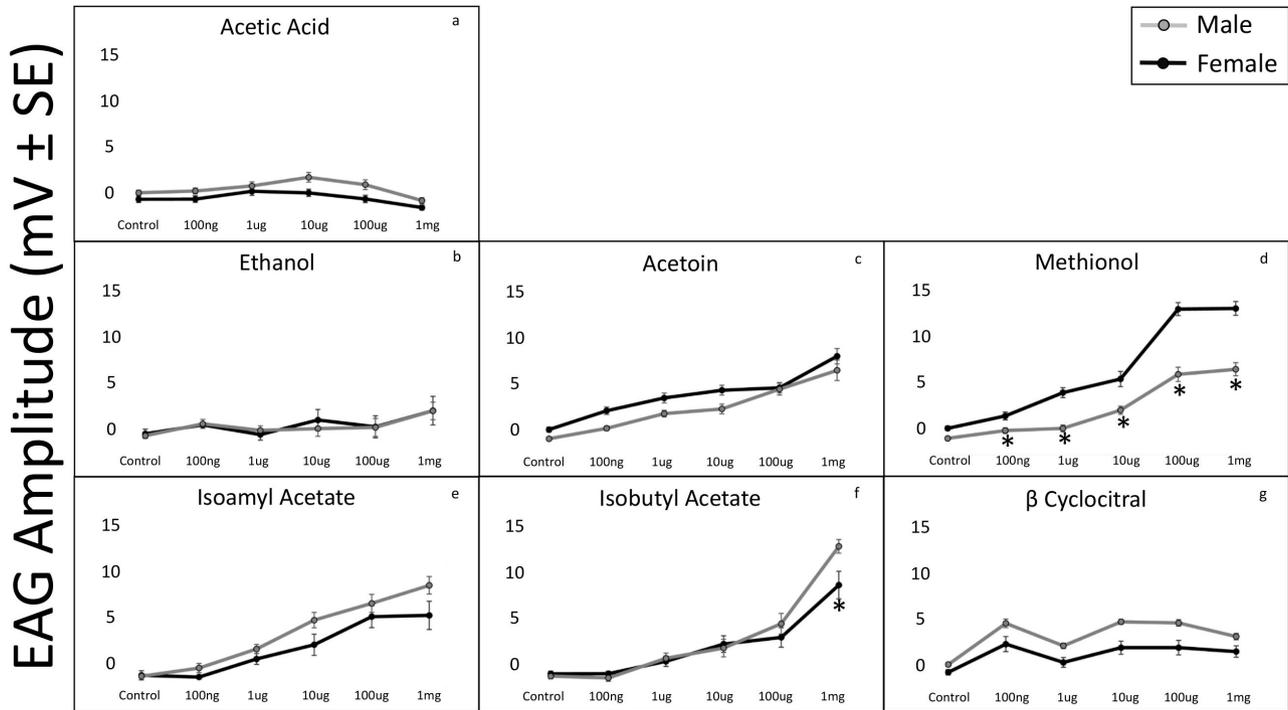
**EAG Assays**

*Drosophila suzukii* antennae responded in a dose-dependent manner to acetoin, methionol, isoamyl acetate, and isobutyl acetate (Fig. 1), indicating antennal sensitivity to these volatiles. There were some differences in the antennal responses between male and female flies. Female antennae were more sensitive to all five concentrations of methionol compared to male antennae ( $\chi^2 = 141.2$ ;  $df = 11$ ,  $P < 0.001$ ) (Fig. 1d), and male antennae were more sensitive to the

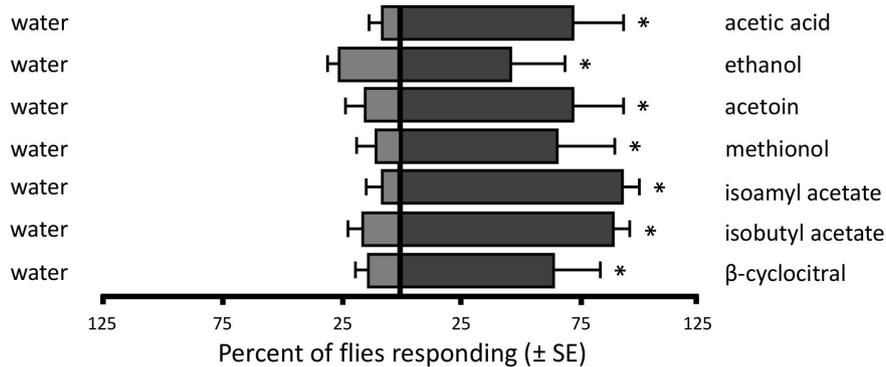
highest concentration (1 mg) of isobutyl acetate ( $\chi^2 = 104.2$ ;  $df = 11$ ,  $P < 0.001$ ) (Fig. 1f).

**Individual-Compound Behavioral Assays**

In choice assays, adult *D. suzukii* were significantly more attracted to each of the individual compounds compared to the water controls (acetic acid:  $t = 3.55$ ,  $df = 4$ ,  $P = 0.02$ , nonresponders [mean % ± SE] =  $22 \pm 6.63$ ; ethanol:  $t = 4.47$ ,  $df = 4$ ,  $P = 0.01$ , nonresponders =  $22 \pm 5.83$ ; acetoin:  $t = 3.01$ ,  $df = 4$ ,  $P = 0.04$ , nonresponders =  $38 \pm 13.93$ ; methionol:  $t = 2.86$ ,  $df = 4$ ,  $P = 0.05$ , nonresponders =  $30 \pm 13.42$ ; isoamyl acetate:  $t = 8.23$ ,  $df = 4$ ,  $P = 0.001$ , nonresponders =  $36 \pm 11.22$ ; isobutyl acetate:  $t = 6.52$ ,  $df = 4$ ,  $P = 0.003$ , nonresponders =  $46 \pm 6.78$ ;  $\beta$  cyclocitral:  $t = 3.55$ ,  $df = 4$ ,  $P = 0.02$ , nonresponders =  $20 \pm 10.49$ ) (Fig. 2).



**Fig. 1.** EAG response curves of male and female *Drosophila suzukii* to seven host-plant-related odors (a-g). EAG amplitudes are presented as non-transformed antennal depolarizations (mV, mean ± SE). Each compound, at each of the five concentrations, was tested on 15 male and 15 female flies. Significant differences between sexes are noted by asterisks ( $P \leq 0.05$ ).



**Fig. 2.** Attraction of adult *Drosophila suzukii* to seven individual host-plant-related odors compared to water controls. Each horizontal bar is the mean percent (±SE) of five male and five female flies (sex data pooled) entering one of the two rearing-tube traps after 48 h.  $N = 5$ . An asterisk indicates significant differences between host odor and the water control ( $P \leq 0.05$ ); ns = not significant.

### Single-Lure Behavioral Assays

In the single-lure behavioral assays, *D. suzukii* flies were significantly more attracted to the positive yeast plus sugar control ( $t = 5.38$ ,  $df = 3$ ,  $P = 0.01$ , nonresponders [mean %  $\pm$  SE] =  $13.33 \pm 7.07$ ) and to the Fermentation lure mixture ( $t = 3.44$ ,  $df = 3$ ,  $P = 0.04$ , nonresponders =  $18.33 \pm 7.26$ ) compared to the blank controls (Fig. 3). The *H. uvarum* lure ( $t = 1.56$ ,  $df = 3$ ,  $P = 0.22$ , nonresponders =  $38.89 \pm 14.95$ ) and the Leaf lure ( $t = 0.47$ ,  $df = 3$ ,  $P = 0.65$ , nonresponders =  $37.78 \pm 9.49$ ) were not more attractive than the blank controls (Fig. 3).

### Combined-Lure Behavioral Assays

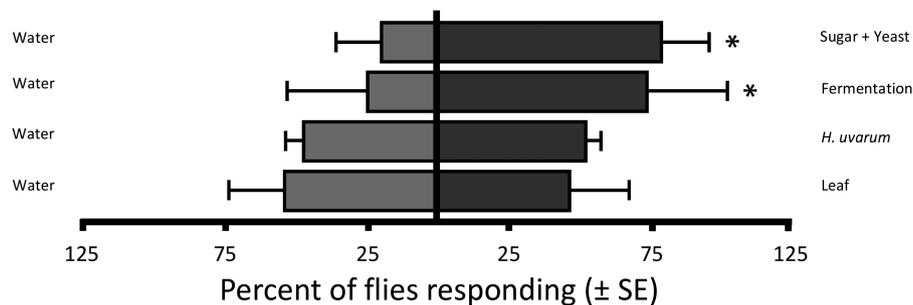
The addition of the Leaf and *H. uvarum* lure compounds to the Fermentation lure did not increase the Fermentation lure's attractiveness to *D. suzukii* flies compared to the Fermentation lure alone. In fact, the addition of 1 ml ( $t = 5.81$ ,  $df = 5$ ,  $P = 0.002$ , nonresponders [mean %  $\pm$  SE] =  $6.11 \pm 2.34$ ) and 100  $\mu$ l of the two *H. uvarum* lure compounds ( $t = 3.59$ ,  $df = 5$ ,  $P = 0.02$ , nonresponders =  $7.22 \pm 3.38$ ), and 500  $\mu$ l ( $t = 5.38$ ,  $df = 5$ ,  $P = 0.01$ , nonresponders =  $3.33 \pm 2.72$ ) of isobutyl acetate to the Fermentation lure decreased its attraction compared to the Fermentation lure alone (Fig. 4). The addition of 1 ml of the Leaf lure ( $t = 2$ ,  $df = 5$ ,  $P = 0.1$ , nonresponders =  $15.56 \pm 7.29$ ), 500  $\mu$ l of the *H. uvarum* lure plus 500  $\mu$ l of the Leaf lure ( $t = 1.7$ ,  $df = 5$ ,  $P = 0.15$ , nonresponders =  $11.11 \pm 3.41$ ), 500  $\mu$ l of the *H. uvarum* lure ( $t = 1.5$ ,  $df = 5$ ,  $P = 0.19$ , nonresponders =  $7.22 \pm 2.5$ ), and 500  $\mu$ l of isoamyl acetate ( $t = 1.28$ ,  $df = 5$ ,  $P = 0.25$ , nonresponders =  $3.89 \pm 2$ ) to the Fermentation lure neither increased nor decreased their attractiveness compared to the Fermentation lure alone (Fig. 4).

### Field Behavioral Assays

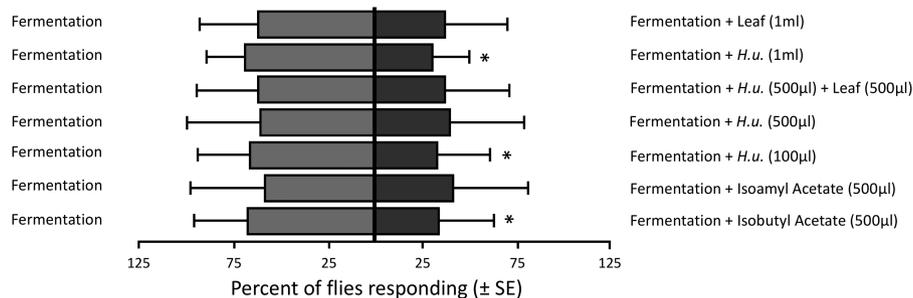
#### Single Lures

During the 2016 field season, the yeast plus sugar bait and the Fermentation lure captured the most *D. suzukii* flies in highbush blueberry ( $\chi^2 = 664.6$ ;  $df = 4$ ,  $P < 0.001$ ,  $N = 1,125$ ), lowbush blueberry ( $\chi^2 = 124.30$ ;  $df = 4$ ,  $P < 0.001$ ,  $N = 130$ ), tart cherry ( $\chi^2 = 80.07$ ;  $df = 4$ ,  $P < 0.001$ ,  $N = 200$ ), and in blackberry and raspberry fields ( $\chi^2 = 51.16$ ;  $df = 4$ ,  $P < 0.001$ ,  $N = 260$ ) (Table 2). In general, trap selectivity for all lure types across all fruit types was relatively low and did not exceed 50% *D. suzukii* (Table 2). Significantly more mature eggs were dissected from female flies captured in traps baited with the Fermentation lure in highbush blueberry ( $\chi^2 = 22.51$ ;  $df = 4$ ,  $P < 0.001$ ), the Leaf lure and the sugar plus yeast bait in lowbush blueberry ( $\chi^2 = 18.11$ ;  $df = 4$ ,  $P < 0.001$ ), and the sugar plus yeast bait in raspberry ( $\chi^2 = 15.98$ ;  $df = 4$ ,  $P < 0.003$ ) (Supp Table S2 [online only]).

In New Jersey highbush blueberry, the Fermentation lure and the sugar and yeast bait captured more *D. suzukii* flies than the *H. uvarum* and Leaf lures and the blank control during the 2016 growing season ( $\chi^2 = 82.02$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 40$ ) (Table 3). Similarly, the Fermentation lure and the sugar and yeast bait captured more flies than the other lures during the off-season; however, the Leaf lure captured more flies than the *H. uvarum* lure and the blank control ( $\chi^2 = 322.2$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 110$ ) (Table 3). Male *D. suzukii* were also more attracted to the *H. uvarum* lure than the control during the off-season. During the 2016–2017 off-season, the Leaf lure captured the largest proportion of *D. suzukii* flies at 45% (Table 3). There was no difference in the number of mature eggs dissected from female flies among lure treatments during



**Fig. 3.** Attraction of adult *Drosophila suzukii* to four different lure combinations compared to blank (no lure) controls. Each horizontal bar is the mean percent ( $\pm$ SE) of 30 adult flies (sex data pooled) entering one of the deli cup traps after 24 h. Yeast = *Saccharomyces cerevisiae*.  $N = 4$ . An asterisk indicates significant differences between host odor and the blank control ( $P \leq 0.05$ ); ns = not significant.



**Fig. 4.** Attraction of adult *Drosophila suzukii* to seven different lure combinations, prepared according to Table 1 formulations, compared to the fermentation lure. Each horizontal bar is the mean percent ( $\pm$ SE) of 30 adult flies (sex data pooled) entering one of the deli cup traps after 24 h. *H.u.* = *H. uvarum*.  $N = 6$ . An asterisk indicates significant differences between host odor and the water control ( $P \leq 0.05$ ); ns = not significant.

**Table 2.** Mean ( $\pm$ SE) total, male, female captures per week, and proportion of *Drosophila suzukii* flies across all sites for the 2016–2017 trapping data

State(s), fruit type	Treatment	Total	Male	Female	Trap selectivity
MI, NC, NJ, NY, OR, highbush blueberry ( $n = 725$ )	Control	0.31 $\pm$ 0.1b	0.07 $\pm$ 0.03b	0.24 $\pm$ 0.07b	0.31 $\pm$ 0.08bc
	Fermentation	185.1 $\pm$ 50.17a	83.81 $\pm$ 22.4a	101.1 $\pm$ 28.2a	0.52 $\pm$ 0.06a
	Leaf	124.3 $\pm$ 25.62a	67.38 $\pm$ 16a	56.96 $\pm$ 10a	0.31 $\pm$ 0.02b
	Sugar + yeast	206.6 $\pm$ 43.53a	99.98 $\pm$ 22.2a	106.6 $\pm$ 21.3a	0.58 $\pm$ 0.05a
	<i>H. uvarum</i>	16.02 $\pm$ 14.1b	7.81 $\pm$ 7.31b	8.21 $\pm$ 6.79b	0.23 $\pm$ 0.03c
ME, lowbush blueberry ( $n = 130$ )	Control	0.65 $\pm$ 0.34cd	0.15 $\pm$ 0.12c	0.5 $\pm$ 0.24d	0.49 $\pm$ 0.15a
	Fermentation	143.4 $\pm$ 93.1bc	67.38 $\pm$ 45.28ab	76.03 $\pm$ 47.9bc	0.49 $\pm$ 0.11a
	Leaf	77.96 $\pm$ 37b	29.61 $\pm$ 13.77b	48.34 $\pm$ 24.1b	0.20 $\pm$ 0.07b
	Sugar + yeast	358.84 $\pm$ 183a	160.7 $\pm$ 83.43a	198 $\pm$ 101.5a	0.64 $\pm$ 0.08a
	<i>H. uvarum</i>	0.04 $\pm$ 0.03d	0	0.04 $\pm$ 0.03d	0.01 $\pm$ 0.01c
NC, NJ, MI, blackberry and raspberry ( $n = 428$ )	Control	14.66 $\pm$ 3.08bc	3.67 $\pm$ 1.04bc	11 $\pm$ 2.12bc	0.34 $\pm$ 0.05bc
	Fermentation	65.73 $\pm$ 16.1b	26.18 $\pm$ 7.18b	39.8 $\pm$ 9.13b	0.45 $\pm$ 0.03b
	Leaf	0.08 $\pm$ 0.04d	0.03 $\pm$ 0.03d	0.05 $\pm$ 0.03d	0.16 $\pm$ 0.09d
	Sugar + yeast	309.9 $\pm$ 76.2a	140.3 $\pm$ 39.6a	169.5 $\pm$ 37.5a	0.62 $\pm$ 0.03a
	<i>H. uvarum</i>	9.95 $\pm$ 3.21c	2.98 $\pm$ 1.32cd	6.97 $\pm$ 1.97c	0.19 $\pm$ 0.04cd
MI, tart cherry ( $n = 192$ )	Control	–	–	–	–
	Fermentation	78.27 $\pm$ 31.77ab	36.66 $\pm$ 15.2b	41.6 $\pm$ 16.63ab	0.56 $\pm$ 0.09a
	Leaf	18.06 $\pm$ 3.38b	6.63 $\pm$ 1.42b	11.43 $\pm$ 2.13b	0.14 $\pm$ 0.02b
	Sugar + yeast	226.7 $\pm$ 124.7a	93.14 $\pm$ 48.3a	133.6 $\pm$ 76.85a	0.55 $\pm$ 0.09a
	<i>H. uvarum</i>	1.42 $\pm$ 1.35b	0.13 $\pm$ 0.12c	1.29 $\pm$ 1.23c	0.07 $\pm$ 0.04b
All states, all fruit types ( $n = 1,475$ )	Control	5.56 $\pm$ 1.25c	1.38 $\pm$ 0.4c	4.17 $\pm$ 0.91c	0.35 $\pm$ 0.04c
	Fermentation	105.2 $\pm$ 17.9b	46.21 $\pm$ 8.19b	59.23 $\pm$ 9.96b	0.48 $\pm$ 0.02b
	Leaf	88.12 $\pm$ 16.9b	46.49 $\pm$ 10.5b	41.63 $\pm$ 6.79b	0.26 $\pm$ 0.02c
	Sugar + yeast	260.1 $\pm$ 42a	118.3 $\pm$ 19.8a	141.8 $\pm$ 22.8a	0.60 $\pm$ 0.02a
	<i>H. uvarum</i>	11.96 $\pm$ 8.94c	5.452 $\pm$ 4.63c	6.515 $\pm$ 4.31c	0.19 $\pm$ 0.02d

NY = New York; NJ = New Jersey; MI = Michigan; NC = North Carolina; OR = Oregon; ME = Maine. Controls contained no lure. Yeast = *Saccharomyces cerevisiae*. Values followed by the same letter are not significantly different ( $\alpha = 0.05$ ).

**Table 3.** Mean ( $\pm$ SE) total, male, female captures per week, and proportion *Drosophila suzukii* across New Jersey (NJ) highbush blueberry sites for the 2016–2017 and 2017–2018 trapping for in and out of season data

Year, season	Treatment	Total	Male	Female	Trap selectivity
NJ, 2016–2017, highbush blueberry, in-season ( $N = 40$ )	Control	0.06 $\pm$ 0.05b	0.03 $\pm$ 0.03b	0.03 $\pm$ 0.03b	0.4 $\pm$ 0.24b
	Fermentation	42.07 $\pm$ 10.95a	22.20 $\pm$ 6.08a	21.37 $\pm$ 6.49a	0.05 $\pm$ 0.01a
	Leaf	0.1 $\pm$ 0.05b	0 $\pm$ 0b	0.10 $\pm$ 0.05b	0.25 $\pm$ 0.13a
	Sugar + yeast	34.17 $\pm$ 9.36a	18.4 $\pm$ 5.38a	15.76 $\pm$ 4.72a	0.11 $\pm$ 0.02a
	<i>H. uvarum</i>	0.17 $\pm$ 0.08b	0.06 $\pm$ 0.04b	0.10 $\pm$ 0.07b	0.24 $\pm$ 0.12b
NJ, 2016–2017, highbush blueberry, off-season ( $N = 110$ )	Control	0.08 $\pm$ 0.05c	0.01 $\pm$ 0.01a	0.08 $\pm$ 0.05c	0.12 $\pm$ 0.05b
	Fermentation	1,816.13 $\pm$ 342.04a	895.26 $\pm$ 172.7d	967.44 $\pm$ 182.6a	0.39 $\pm$ 0.03a
	Leaf	8.04 $\pm$ 2.89b	3.68 $\pm$ 1.38c	4.52 $\pm$ 1.58b	0.45 $\pm$ 0.05a
	Sugar + yeast	465.11 $\pm$ 74.8a	212.56 $\pm$ 41.41c	256.72 $\pm$ 39.5a	0.38 $\pm$ 0.03a
	<i>H. uvarum</i>	5.04 $\pm$ 4.99c	2.42 $\pm$ 2.42b	2.65 $\pm$ 2.66c	0.07 $\pm$ 0.03b
NJ, 2017–2018, highbush blueberry, in-season ( $N = 40$ )	Control	0.06 $\pm$ 0.06c	0 $\pm$ 0a	0.06 $\pm$ 0.06c	0.5 $\pm$ 0.5ab
	Fermentation	47.2 $\pm$ 7.39a	25.76 $\pm$ 4.79b	21.14 $\pm$ 3.14a	0.14 $\pm$ 0.02a
	Fermentation + leaf	18.93 $\pm$ 3.87a	8.93 $\pm$ 2.21b	10 $\pm$ 2.04ab	0.17 $\pm$ 0.03a
	Fermentation + <i>H. uvarum</i>	23.06 $\pm$ 4.09a	12.66 $\pm$ 2.3b	10.4 $\pm$ 2.14a	0.12 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i> + leaf	6.6 $\pm$ 1.57b	2.8 $\pm$ 0.62b	3.8 $\pm$ 1.12b	0.13 $\pm$ 0.03a
	Sugar + yeast	54.03 $\pm$ 11.33a	24.83 $\pm$ 5.66c	29.2 $\pm$ 7.32a	0.13 $\pm$ 0.02b
NJ, 2017–2018, highbush blueberry, off-season ( $N = 140$ )	Control	0.11 $\pm$ 0.07b	0.08 $\pm$ 0.05b	0.03 $\pm$ 0.03b	0.32 $\pm$ 0.14a
	Fermentation	4,737.9 $\pm$ 1,064.1a	2,686.8 $\pm$ 639.2a	2,051 $\pm$ 435.9a	0.25 $\pm$ 0.02a
	Fermentation + leaf	2,677.7 $\pm$ 677.1a	1,538.9 $\pm$ 401.3a	1,158.7 $\pm$ 296.2a	0.30 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i>	2,385.19 $\pm$ 648.78a	1,211.7 $\pm$ 325.7a	1,191.29 $\pm$ 330a	0.28 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i> + leaf	1,133.3 $\pm$ 262.6a	558.9 $\pm$ 127.6a	591.4 $\pm$ 142.7a	0.26 $\pm$ 0.02a
	Sugar + yeast	2,588.1 $\pm$ 529.7a	1,394.5 $\pm$ 286.5a	1,208.4 $\pm$ 272.2a	0.25 $\pm$ 0.02a

Controls contained no lure. Yeast = *Saccharomyces cerevisiae*. Values followed by the same letter are not significantly different ( $\alpha = 0.05$ ).

the growing season ( $\chi^2 = 3.72$ ;  $df = 4$ ,  $P = 0.29$ ) or during the off-season ( $\chi^2 = 3.41$ ;  $df = 4$ ,  $P = 0.33$ ) (Supp Table S3 [online only]). In 2016–2017, there was an interaction between seasons ( $\chi^2 = 7.61$ ,  $P = 0.006$ ) and lure type ( $\chi^2 = 19.76$ ,  $P < 0.001$ ) on number of mature eggs, indicating that the response of mature females to the lures varied between the growing season and the off-season (Supp Table S3 [online only]).

#### Combined Lures

Fly captures for the 2017 season, when different lure types were combined, were more variable across fruit types compared to the 2016 field season when only individual lure types were deployed (Table 4). In highbush blueberry, the yeast plus sugar positive control bait captured the most *D. suzukii* flies, whereas the addition of the *H. uvarum* and Leaf lures to the Fermentation lure significantly reduced fly captures compared to the Fermentation lure alone ( $\chi^2 = 95.76$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 167$ ) (Table 3). The Fermentation lure and the yeast plus sugar positive control lure captured similar numbers of flies, the Fermentation lure plus the Leaf lure and the Fermentation lure plus the *H. uvarum* lure captured similar numbers, and the addition of both the *H. uvarum* and Leaf lures significantly reduced fly attraction to the Fermentation lure in lowbush blueberry ( $\chi^2 = 227.76$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 283$ ) and in blackberry and raspberry ( $\chi^2 = 175.8$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 144$ ) (Table 4). In blackberry and raspberry, the sugar plus

yeast positive control lure captured the greatest number of flies and the Fermentation lure plus the *H. uvarum* and Leaf lures captured the fewest number of flies ( $\chi^2 = 127.38$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 678$ ) (Table 4). In cherry, the Fermentation lure plus the *H. uvarum* and Leaf lures also captured the fewest number of *D. suzukii*, and the Fermentation lure and the sugar plus yeast positive control lure captured the most flies ( $\chi^2 = 112.5$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 646$ ) (Table 4). Across all states and crops, the sugar plus yeast positive control lure captured the greatest number of flies and the Fermentation lure alone captured significantly more *D. suzukii* than when the Fermentation lure was combined with the *H. uvarum* and Leaf lures ( $\chi^2 = 352.41$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 1,679$ ) (Table 4). In general, trap selectivity for all lure types and across all fruit types did not exceed 50% *D. suzukii* except in lowbush blueberry where all lures, except for the Fermentation lure plus the *H. uvarum* and Leaf lures captured between 55 and 69% *D. suzukii* (Table 4). There was no difference in the number of mature eggs dissected from female flies among lure treatments in highbush and lowbush blueberry ( $\chi^2 = 12.25$ ;  $df = 5$ ,  $P < 0.001$ ). However, females dissected in raspberry attracted to the yeast and sugar positive control bait contained more mature eggs than the four treatment lures ( $\chi^2 = 112.94$ ;  $df = 5$ ,  $P = 0.03$ ) (Supp Table S4 [online only]). Due to a low number of females dissected ( $N = 4$ ) in the control, 100% of these females were mated, and one outlier containing a large egg-load, the blank control in the 2017

**Table 4.** Mean ( $\pm$ SE) total, male, female captures per week, and proportion of *Drosophila suzukii* across all sites for the 2017–2018 trapping data

State(s), fruit type	Treatment	Total	Male	Female	Trap selectivity
NJ, OR, highbush blueberry ( $n = 167$ )	Control	0.04 $\pm$ 0.04d	0 $\pm$ 0	0.01 $\pm$ 0.01d	0.33 $\pm$ 0.33a
	Fermentation	32.91 $\pm$ 5.81ab	17.42 $\pm$ 3.64ab	0.87 $\pm$ 0.09ab	0.1 $\pm$ 0.01a
	Fermentation + leaf	18.93 $\pm$ 3.88b	8.93 $\pm$ 2.21bc	0.77 $\pm$ 0.1b	0.17 $\pm$ 0.03a
	Fermentation + <i>H. uvarum</i>	23.06 $\pm$ 4.09ab	12.66 $\pm$ 2.3ab	0.78 $\pm$ 0.1b	0.12 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i> + leaf	6.6 $\pm$ 1.57c	2.8 $\pm$ 0.62c	0.47 $\pm$ 0.07c	0.13 $\pm$ 0.03a
	Sugar + Yeast	54.03 $\pm$ 11.33a	24.83 $\pm$ 5.66a	1.05 $\pm$ 0.13a	0.13 $\pm$ 0.02a
ME, lowbush blueberry ( $n = 144$ )	Control	0.46 $\pm$ 0.26d	0.08 $\pm$ 0.06d	0.38 $\pm$ 0.22d	0.69 $\pm$ 0.16a
	Fermentation	1,066 $\pm$ 221.3a	335 $\pm$ 99.65a	731 $\pm$ 144.9a	0.55 $\pm$ 0.05a
	Fermentation + leaf	366.12 $\pm$ 109.4b	102 $\pm$ 31.76b	264.1 $\pm$ 86.68b	0.54 $\pm$ 0.05a
	Fermentation + <i>H. uvarum</i>	294.83 $\pm$ 133.7b	122.5 $\pm$ 80.15bc	172.3 $\pm$ 60.92b	0.50 $\pm$ 0.06a
	Fermentation + <i>H. uvarum</i> + leaf	135.66 $\pm$ 62.7c	32.29 $\pm$ 12.53c	103.3 $\pm$ 52.82c	0.45 $\pm$ 0.05a
	Sugar + yeast	1,048.2 $\pm$ 184.7a	296.7 $\pm$ 73.79a	751.5 $\pm$ 129.5a	0.57 $\pm$ 0.06a
NC, NY, MI, blackberry and raspberry ( $n = 678$ )	Control	0.19 $\pm$ 0.07e	0.05 $\pm$ 0.03d	0.13 $\pm$ 0.04e	0.38 $\pm$ 0.09ab
	Fermentation	53.28 $\pm$ 12.26b	26.04 $\pm$ 7.36b	27.23 $\pm$ 5.28b	0.3 $\pm$ 0.03ab
	Fermentation + leaf	22.69 $\pm$ 5.19cd	10.92 $\pm$ 2.8bc	11.76 $\pm$ 2.5cd	0.26 $\pm$ 0.03b
	Fermentation + <i>H. uvarum</i>	37.67 $\pm$ 8.85c	16.78 $\pm$ 4.46b	20.88 $\pm$ 4.55c	0.31 $\pm$ 0.03ab
	Fermentation + <i>H. uvarum</i> + leaf	14.15 $\pm$ 3.81d	5.93 $\pm$ 1.79c	8.36 $\pm$ 2.1d	0.24 $\pm$ 0.03b
	Sugar + yeast	165.8 $\pm$ 35.02a	62.03 $\pm$ 13.9a	103.7 $\pm$ 21.8a	0.38 $\pm$ 0.03a
MI, OR cherry ( $n = 646$ )	Control	0.81 $\pm$ 0.35d	0.39 $\pm$ 0.24d	0.42 $\pm$ 0.14d	0.25 $\pm$ 0.06a
	Fermentation	58.31 $\pm$ 12.5a	37.69 $\pm$ 9.95a	21.71 $\pm$ 3.27a	0.37 $\pm$ 0.04a
	Fermentation + leaf	30.07 $\pm$ 7.87bc	19.27 $\pm$ 5.77b	11.08 $\pm$ 2.61bc	0.32 $\pm$ 0.04a
	Fermentation + <i>H. uvarum</i>	24.87 $\pm$ 5.82b	16.59 $\pm$ 4.68ab	8.5 $\pm$ 1.39b	0.38 $\pm$ 0.03a
	Fermentation + <i>H. uvarum</i> + leaf	9 $\pm$ 2.64c	5.56 $\pm$ 1.92c	3.61 $\pm$ 0.83c	0.32 $\pm$ 0.04a
	Sugar + yeast	79.2 $\pm$ 20.6a	45.27 $\pm$ 16.1a	35.43 $\pm$ 6.12a	0.34 $\pm$ 0.03a
All states, all fruit types ( $n = 1,635$ )	Control	0.42 $\pm$ 0.14e	0.17 $\pm$ 0.09d	0.25 $\pm$ 0.05e	0.33 $\pm$ 0.05a
	Fermentation	135.8 $\pm$ 25.26b	54.73 $\pm$ 10.6a	82.01 $\pm$ 16.72b	0.31 $\pm$ 0.02a
	Fermentation + leaf	55.15 $\pm$ 11.65c	21.94 $\pm$ 4.02b	33.40 $\pm$ 8.74c	0.30 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i>	53.49 $\pm$ 13.03c	25.52 $\pm$ 7.58b	28.16 $\pm$ 6.22c	0.33 $\pm$ 0.02a
	Fermentation + <i>H. uvarum</i> + leaf	21.91 $\pm$ 6.07d	7.76 $\pm$ 1.58c	14.38 $\pm$ 4.96d	0.28 $\pm$ 0.02a
	Sugar + yeast	197 $\pm$ 28.05a	72.16 $\pm$ 11.4a	126.3 $\pm$ 18.91a	0.35 $\pm$ 0.02a

NY = New York; NJ = New Jersey; MI = Michigan; NC = North Carolina; OR = Oregon; ME = Maine. Controls contained no lure. Yeast = *Saccharomyces cerevisiae*. Values followed by the same letter are not significantly different ( $\alpha = 0.05$ ).

raspberry field season, contained the greatest number of mature eggs dissected (Supp Table S4 [online only]).

In New Jersey, although the Fermentation lure captured the highest numbers of *D. suzukii* flies during the 2017 growing season, the number of captured flies was not significantly different than from the number captured with the Fermentation lure plus the *H. uvarum* lure and the Fermentation plus the Leaf lure, but were significantly higher than the Fermentation lure plus the *H. uvarum* and Leaf lures and also the control; the Fermentation lure plus the *H. uvarum* and Leaf lures captured more flies than the blank control ( $\chi^2 = 110.96$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 674$ ) (Table 3). Similarly, the Fermentation lure captured a greater number of *D. suzukii* flies than the control in the 2017–2018 off-season, but trap captures were not statistically different from captures in traps with all the lure combinations or the yeast plus sugar bait ( $\chi^2 = 110.96$ ;  $df = 5$ ,  $P < 0.001$ ,  $N = 674$ ). The proportion of *D. suzukii* flies captured across all lure types during the 2017 growing season and the 2017–2018 off-season was similar and relatively low (between 12 and 32%) (Table 3). There was no difference in the number of mature eggs among lure treatments during the growing season ( $\chi^2 = 5.32$ ;  $df = 5$ ,  $P = 0.26$ ) and the off-season ( $\chi^2 = 3.86$ ;  $df = 5$ ,  $P = 0.57$ ) (Supp Table S3 [online only]). In 2017–2018, only ‘season’ affected the number of mature eggs such that the number of mature eggs per female was greater during the growing season than in the off-season ( $\chi^2 = 31.47$ ,  $P \leq 0.001$ ).

## Discussion

This study adds to the growing literature on our understanding of the chemical cues used by *D. suzukii* adults in host-plant and mate location. We found that 1) adding two *H. uvarum* yeast compounds, isoamyl acetate and isobutyl acetate (*H. uvarum* lure), and a leaf odor,  $\beta$ -cyclocitral (Leaf lure), does not increase *D. suzukii* fly attraction to a Fermentation lure, which is composed of four fermentation compounds (acetic acid, ethanol, acetoin, and methionol); and 2) contrary to our expectations, cues from different sources appear to interfere with each other. Combinations of the Fermentation lure plus the *H. uvarum* lure (isoamyl acetate and isobutyl acetate) and the Leaf lure ( $\beta$ -cyclocitral), in some cases, reduced *D. suzukii* fly attraction compared to the Fermentation lure alone under the experimental conditions that we tested. It may be that different lure doses, lure release rates, and blend ratios will yield different results than we found in our behavioral and field experiments. Future work should investigate, both in the laboratory and field, the minimum dose and ratio of isoamyl acetate, isobutyl acetate, and  $\beta$ -cyclocitral that are required to interfere with *D. suzukii* fly attraction to the Fermentation lure.

There were some agreements but also some discrepancies between our physiological (EAG) and behavioral results. *Drosophila suzukii* responses to the Fermentation lure compounds, acetic acid, ethanol, acetoin, and methionol, were the most consistent across assays. All individual and the mixture of fermentation odors tested elicited behavioral responses in *D. suzukii* males and females in the laboratory and field. Two of these compounds, acetoin and methionol, also elicited strong EAG responses in a dose-dependent manner; although females responded more strongly than males to methionol. In contrast, *D. suzukii* flies were attracted to acetic acid and ethanol but the antennal response to these odors was weak, similar to results reported by Cha et al. (2012). One plausible explanation is that, because these two compounds are highly volatile,

they could have evaporated before they were puffed. In the laboratory, the *H. uvarum* yeast odors isoamyl acetate and isobutyl acetate were attractive to *D. suzukii* flies individually but not as a blend. These results were similar in the field where the mixture of isoamyl acetate and isobutyl acetate (*H. uvarum* lure) did not attract flies during the growing season, when fruit and leaves were present on the plants. However, attraction of males to the *H. uvarum* lure increased during the off-season, indicating that background odors might be important in the response of *D. suzukii* to these odors. There were also some inconsistencies in the *D. suzukii* response to  $\beta$ -cyclocitral (Leaf lure). For instance, although  $\beta$ -cyclocitral elicited weak EAG responses in *D. suzukii*, it was attractive to flies in small arenas (deli containers) but not in large cages. Similar to the *H. uvarum* lure, *D. suzukii* attraction to the Leaf lure ( $\beta$ -cyclocitral) was weak during the growing season but increased during the off-season. These inconsistencies could be due to differences in dose of compounds and conditions used in EAG and behavioral assays and between lab and field assays.

Although attraction of *D. suzukii* to the *H. uvarum* and Leaf lures was overall weak as compared with that to the Fermentation lure and the yeast plus sugar bait, we provide some evidence that this response is context-dependent. Male attraction to the *H. uvarum* lure increased during the off-season in New Jersey blueberry, when leaves and fruit were absent from the fields. Likewise, both male and female fly attraction to the Leaf lure increased during the off-season. These results highlight the fact that the behavioral response of *D. suzukii* flies to host-related volatile compounds, such as those from yeasts and leaves, likely depend on background odors. Further studies should address the role of background odors, i.e., presence of fruits and/or leaves, on the response of *D. suzukii* flies to various odor cues.

The roles of yeast and leaf odors in *D. suzukii* foraging behaviors (i.e., as cues for food, mate, and oviposition site location) remain unclear. Keeseey et al. (2015) suggested that gravid female *D. suzukii* are initially attracted to leaf material, i.e.,  $\beta$ -cyclocitral, for host-plant location and then exploit fresh fruit odors for oviposition or mating site detection. Yeast odors likely attract mated *D. suzukii* for protein feeding and egg maturation purposes (Karageorgi et al. 2017). Indeed, based on the number of mature eggs, females were sexually mature when responding to the *H. uvarum* volatiles isoamyl acetate and isobutyl acetate, and the leaf volatile  $\beta$ -cyclocitral in the field. However, when presented together as a lure, these odors may conflict and be responsible for the decreased attraction that was observed across all fruit types. To our knowledge, this is the first study to report that the combination of non-ecologically relevant odors reduces captures of *D. suzukii* to a blend of compounds that is an effective bait. It should be noted though that the dose of compounds used in both the behavioral and field assays may be outside the biologically relevant range that *D. suzukii* will encounter and additional dose-dependent studies are needed to verify our findings.

Previous studies have also shown that mixtures of individual attractive compounds do not always elicit an increased behavioral response in adult *D. suzukii*. For example, in laboratory behavioral bioassays, Cha et al. (2012) found that the addition of ethyl acetate, ethyl butyrate, 1-hexanol, isoamyl acetate, 2-methylbutyl acetate, and ethyl sorbate to a mixture of acetic acid and ethanol significantly reduced *D. suzukii* fly attraction. Therefore, it is likely that attractive volatiles detected by *D. suzukii* outside an appropriate context may interfere rather than enhance their response towards another attractive cue during foraging for hosts. In contrast, if they are part of an ecologically relevant combination, they may be perceived as an attractive host stimulus (Bruce and Pickett 2011). For example, Jaffe et al. (2018) found that the addition of compounds

in the headspace of apple juice (acetoin, ethyl octanoate, and acetic acid) plus the commercially available Scentry lure, that is composed of acetic acid, ethanol, acetoin, and methionol (Cha et al. 2017), to vinegar and flour fermenting baits do not increase *D. suzukii* fly attraction compared to vinegar and flour fermenting bait alone. However, the addition of the yeast (*S. cerevisiae*) and sugar bait to the Scentry lure additively increased *D. suzukii* attraction in blueberry and raspberry fields. In this case, it may be that fermenting baits produce most of the same compounds as the yeast and sugar bait and the Scentry lure, and thus some of these combinations were redundant. Future work should investigate the behavioral response of *D. suzukii* flies in the laboratory and field to other, possibly more ecologically relevant, odor combinations such as blends of fruit and leaf odors or fruit and yeast odors that likely serve as oviposition cues for *D. suzukii* (Cloonan et al. 2018). Mori et al. (2017) reported, however, that mated *D. suzukii* females seek yeast (*H. uvarum*) for feeding while they seek fruit odors for oviposition; thus, odors from fruit and yeast may not necessarily be compatible.

In summary, as reported in previous studies, we found that the Fermentation lure, composed of acetic acid, ethanol, acetoin, and methionol, alone was still the most attractive blend to *D. suzukii*. In this study, we were unable to improve the sensitivity or selectivity of the Fermentation lure by adding the *H. uvarum* volatiles isoamyl acetate and isobutyl acetate, and the leaf volatile  $\beta$ -cyclocitral, at least under the conditions tested here. However, we report an interesting phenomenon wherein the *H. uvarum* and leaf volatiles may become more effective in attracting *D. suzukii* flies in the off-season. The information presented here will help guide future research investigating more specific and attractive lure blends for *D. suzukii*. For instance, further work is necessary to explain the potential mechanism(s) responsible for the decreased attraction of certain blend combinations in this study. In addition, the role of physiological status of flies, i.e., virgin, mated, satiated, or starved, in their response to various lure combinations should be further investigated in the laboratory as done by Wong et al. (2018). Future studies should also test other odor combinations that may be more ecologically relevant to food- and host-seeking *D. suzukii* behaviors than those tested in this study.

## Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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